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PHYSIOLOGICAL COMPETITION AS A REGULATORY MECHANISM IN MORPHOGENESIS

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INTRODUCTION

THE major purpose of the present paper is to formulate a theory for a regulative principle of developmental processes. In the course of the analysis it is further proposed to examine in some detail the consequences of the principle of physiological dominance and the gradient theory from which it arose. It will be indicated that the deduction of regulation from the gradient concept requires auxiliary assumptions concerning the mechanisms through which gradients affect the course of development. A mechanism first used by Barth (1938) will be generalized and rigorously developed. The development will permit an examination of its adequacy as a regulatory mechanism. The biological field theory will also be considered, with a view to extending the principles of competitive interaction to a field concept. A method for an extension of this kind will be briefly discussed. Finally, it is important to note that the quantitative data on coelenterate regeneration has served as the main guide for the present analysis, although a broader basis is adopted in the discussion wherever possible.

THE PROBLEM: LIMITED REALIZATION

The fact that many pathways leading to different end results exist, and yet the processes of normal development and regeneration follow a particular one is one way of posing the fundamental problem of embryology. Attempts at the solution of this problem become a search for a regulative principle.

It is known, for example, that if the early blastomeres of some eggs are separated, each is capable of giving rise to a complete and perfectly proportioned embryo. Yet in the normal course of events this potentiality is not realized, each blastomere giving rise to but a part of an embryo. The central problem here is to find the regulative mechanism which successfully limits these capabilities.

Numerous experiments have indicated that for organs and organ systems the field capable of differentiating into a particular structure is more extensive than the area which actually forms the organ under normal conditions. Here again a limitation of potentialities is obtained, in that only a fraction of the field potency is realized. Hydranth reconstitution in the coelenterates, entailing as it does the suppression of all but apical hydranths, presents a particularly well-examined instance of such regulation. Though little direct experimental confirmation exists for it, the gradient concept first proposed by Boveri in 1901 and brought to its full development by Child (1941) has of late received wide acceptance. In more or less direct support of the gradient hypothesis, we may cite Adelmann's (1929a, b) work on eye development as well as a detailed study of gradients in coelenterates and planarians by Child and his coworkers, to which we shall return. However,

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it has been the many verifications of its indirect consequences that has been the stimulus for the wide adoption of the gradient viewpoint. But its use in the interpretation of developmental phenomena has not been entirely uncritical. Gradients have been used by not a few authors to explain the partial realization of potencies without any supplementary arguments as to how the latter is effected. Thus, to say that the realization of field potencies in actual development is *localized in the high region of the potency gradient* is little more than a restatement of the observation. It must be emphasized that the existence of two regions with different capabilities for differentiation does not of itself imply the necessary suppression of the one with the lower power to transform. The explanations in terms of gradients alone tacitly make use of this implication, and in so doing lose sight of the crux of the problem, namely, the mechanism involved in the suppression of existent potentialities.

From the available information two concepts emerge which are basically important for the present analysis. The first is the postulated existence of gradients in differentiation power along one or more axes of a morphogenetic field. The second is that as a result of some as yet unknown regulative mechanism, a principle of potency limitation is apparently followed during normal development of organismic pattern. This principle may well be called the *principle of limited realization.*" These two concepts cannot be regarded as isolated or unconnected. Clearly, if one of two regions is to succeed in the completion of a process of which both are capable, it is not conceivable that they both have equal ability to do so. The very fact that one goes to completion and the other does not would indicate that a difference must exist, and if this difference varies in a reasonably continuous fashion, it may well be called a gradient. In other words, the facts would appear to demand that a necessary condition for the suppression of the inhibited group is that some kind of a gradient should exist between it and the successful one. Nevertheless, while a gradient is necessary for a suppression of this nature, it is not sufficient in itself to bring it about. The necessary condition, however, makes the gradient concept a logically indispensable part of any theory which seeks to explain the principle of limitation. This then leaves open the question of what other postulate can be selected which, when used in conjunction with the gradient hypothesis, will make the combination necessary and sufficient conditions for the deduction of regulatory behavior. The central problem may thus be reduced to one of finding a mechanism whereby gradients can be implemented as effective regulatory agents in morphogenesis.

METHODS

Since differentiation is a process taking place in time as well as space, a kinetic analysis will make up a major portion of the present examination. It is important at this point to note the nature of the quantitative data available. When it is desirable to acquire quantitative information on rate or extent of development, it has been customary to select some well-defined stage and measure the time required to reach it. Thus for example, in the regeneration of hydranths in *Tubularia*, the time from cutting to the appearance of a constriction between the hydranth primordium and the rest of the stem has frequently served this purpose. The problem of the interpretation of rates determined in this manner with particular reference to open and closed systems is discussed by Spiegelman and Moog, 1944. In other instances, the actual emergence of the hydranth from the stem has been chosen as the end point of the process. In any case, whatever stage is selected, even though it be the first visible signs of differentiation, it is obvious that a certain amount of differentiation must have preceded it. It is even more obvious that a certain critically minimal amount of differentiation must occur if the organism is to reach some arbitrarily chosen stage.

With this type of data, then, the existence of dominance or the suppression of one of two groups implies only that one of them is capable of reaching a particular stage in development and the other cannot. It does not imply the complete inhibition of differentiation in the dominated group. For this reason a kinetic theory of dominance which seeks to describe the phenomenon in terms of the available data can only do so in terms of the relative amounts of differentiation attained in the interacting groups. That is to say, dominance will be exhibited if it can be shown that as a result of the postulated interaction the dominated group cannot reach either the differentiation level attained by the successful group, nor the level attainable when it is isolated from the dominating one.

The present analysis will not inquire into the origin of regional differences. On the contrary, their existence will constitute the primary assumption of the theory to be developed for potency limitation. Two important questions for which specific answers will be sought are:

1. Admitting the existence of activity gradients, what are the consequences for the development of organismic patterns?
2. What mechanism of a simple nature can be postulated that will provide a reasonable and justifiable explanation for the principle of limitation as manifested by such phenomena as dominance?

The answers to these questions will be obtained for the most part in purely biological terms, a restriction imposed by the almost complete ignorance of the biochemical basis of morphogenesis. It is logically not necessary to make detailed assumptions concerning the nature of the "activity" whose gradient is being postulated. We may with Child call it a gradient of "physiological activity," if nothing further is implied than that gradients in ability to differentiate have been presumed and that these must have a physiological basis. A more precise definition and interpretation will be possible within the formulation of the theory.

THE CONCEPT OF PHYSIOLOGICAL COMPETITION IN DIFFERENTIATION

The interaction theory to be developed in the subsequent sections is based on the following assumptions:

1. All physiologically active biological organisms are open systems (see Reiner and Spiegelman, 1944, for a discussion of the energetics of open systems) through which matter is continually flowing and within which energy is continually being expended to maintain the status quo. (Assumptions 2 and 3 are not strictly independent of 1. The argument necessary to deduce them however would lead us too far from the purposes of the present discussion.)
2. Open systems interact, i.e., influence each other's (physiological) state and activity.
3. Closed systems do not interact in the above sense

To further specify the nature of the biological interaction with which we shall be concerned, we state the following definition of *physiological competition*: Every group of biological units (species, individuals, cells) are in *physiological competition* if,

a. They require and draw upon a common source of food (substrate) and (or)
b. excrete harmful metabolites into a common environment.

Both of the biological interactions mentioned in the above definition are competitive, the first obviously so, while the second may be reduced to a competition for what can be called "biological or physiological space." Every cell (or organism) requires for its continued existence not only the space it occupies physically but also enough of its environment to dilute its waste products below a critically harmful level. It is in this sense that we may speak of competition for space as well as food.

In order to apply the above assumptions and definition to the particular problem of cellular differentiation it is necessary to postulate the following:

4. The transformation of a group of indifferent cells into a more highly specialized tissue requires the synthesis of new structure, and this synthesis involves the expenditure of energy.
5. A mechanism must exist involving the breakdown of some energy-rich substrate to supply the necessary energy.

In these terms, two groups of cells transforming into the same structure and coexisting in the same physiological environment will compete for the energy-rich substrate.

It is the task of the succeeding sections to deduce the consequences of this kind of competition for the transformation, and its kinetics. One of these consequences, because of its importance, may be mentioned here. It follows from assumption 1 that when a structure is complete and no additional material is being synthesized, a steady and minimum supply of the energy-yielding substrate is still necessary to keep the system intact. This dynamic view of structural stability receives strong experimental support from the work of Schoenheimer and his coworkers (1940a). As will be seen, this has important implications for the process of differentiation, for it implies that a fully differentiated structural unit does not, by its completeness, remove itself from the common physiological space.

TRANSFORMATION WITHOUT INTERACTION

Consider a group of cells in a 'neutral' environment and physiologically isolated from any other group going through the same process. Absolute neutrality of the environment as well as complete isolation are of course impossible of attainment, but experimentally, the ideal may be roughly approximated. For the purposes of comparison it is sufficient that some particular set of experimental conditions be selected as standard, and all other data may be compared with the results obtained from it. Let the mass of cells be M. At the beginning of the observations they are all type-n having a mass N. Type-n cells differentiate into type-r, having a mass R at any t. With progressive differentiation N decreases and R increases. We shall for the moment assume that during the period of observation, ordinary growth in mass or numbers does not accompany the differentiation to any significant extent. This assumption, while not entirely necessary, is helpful if the examination is to be focused on the transformation processes.

Since the mass of tissue, M, remains constant, we may write that, throughout the period of observation,

$$M = N + R \tag{1}$$

If the time course of the process is to be studied, a basic assumption governing the kinetics must be made. Let us assume that the rate at which the n-type transforms into the r-type is proportional to N, the mass of the n-type present at any given moment. That this is a reasonable assumption is apparent from the fact that if it is desired to measure rate of differentiation in terms of *mass of tissue transformed per unit of time*, then it would seem that the greater the amount of the original type present, the larger will the measured rate be. This assumption of proportionality leads to the equation

$$\frac{dR}{dt} = bN \tag{2}$$

The b in equation (2) is a constant of proportionality with an important biological interpretation. It will be noted that it represents the ability in terms of mass per unit of time of any group of n-cells to transform into r-cells. Complete realization of inherent potentiality for differentiation is here achieved, since the condition of physiological isolation implies the absence of all restraints on the processes taking place in the isolated system. Consequently, b may be taken as a measure of this inherent potentiality as evaluated in physiological isolation. In general, then, the ability to differentiate will vary directly with b, so that the larger the value of b, the greater is the potentiality for differentiation.

An important feature of this biological constant is that its value is obtained from a standard isolated state and as such is a characteristic of a group of cells independent of the environment in which they happen to find themselves. In this way, environmental modifications of differentiation potentiality can be considered separately. In a multicellular organism, b will vary from one group of cells to another, in general decreasing from the anterior to the posterior regions. It may here be stated that if physiological gradients are considered in terms of ability to differentiate, then the gradient in the constant b from point to point in the animal must be taken into account. We may call this parameter the "inherent differentiation potential."

Particular attention must be paid to the end process when differentiation is complete. To study this as well as the other parts of the transformation, it is sufficient to integrate equation (2) and observe what occurs when t is allowed to increase. Since two distinct variables are varying with t, equation (2) cannot be integrated directly. However, by means of (1) we may write

$$\frac{dR}{dt} = b(M - R) \tag{3}$$

This is integrated to yield

$$ln\ C - ln\ (M - R) = bt$$

where C is a constant of integration, the value of which is determined by the initial conditions. Passing to natural numbers, we obtain

$$M - R = Ce^{-bt} \tag{4}$$

For a general evaluation of C we may assume that at zero time, R, the mass of r-type cells has the value R_O so that

$$M - R = (M - R_O)e^{-bt}$$

For the special case being considered, in which the experiment is started with no r-type cells, R_O becomes zero and C reduces to M. For this case we may then write

$$R = M(1 - e^{-bt}) \tag{5}$$

Equation (5) gives the complete time course of the phenomenon. With increasing t, the exponential becomes smaller and subsequently becomes negligible, so that R approaches M in magnitude. When R reaches M, no further changes occur in the system with the passage of time. It is apparent that equation (5) predicts that the process of differentiation will stop only when all of the n-cells have transformed into the r-type. This, perhaps, can be more clearly seen from equation (3) where, unless b is zero, $\frac{dR}{dt}$ cannot become zero until R becomes equal to M in value, the total mass of tissue.

This prediction of complete potency realization is of course not surprising in complete physiological isolation, where no resistance to differentiation exists. However, a complete absence of environmental inhibition is of course rarely obtained, and a description more closely approximating reality would take such factors into account. In addition, greater generality and flexibility would be obtained by an analysis permitting some fraction of the total mass of cells originally present to remain undifferentiated. We may denote this fraction by

$$\epsilon = \frac{K}{M} \tag{6}$$

where K is the mass which actually transforms into the r-type, $(M - K)$ remaining undifferentiated. The number ϵ varies between zero and one and is characteristic of a particular tissue under standard external conditions. In general, it will vary with changing environmental circumstances. Since it is a measure of the non-realization of potentialities due to environmental resistance, it may be called the "environmental coefficient of resistance." The situation described by equation (5) becomes then a special case where ϵ is unity and K is consequently equal to M.

There are further implications in equation (3) which would bear closer examination. The b in this equation is a constant and does not vary with time. No objections can be raised against this implicit assumption if all the cells transform simultaneously. However, if it is desired to examine a less restricted condition where various cells in the population take different amounts of time to complete the transformation, a serious difficulty arises. A time-independent b for this case would imply that the differentiation potential of the cells which transform later in the process is the same as that of those which did so earlier. This is patently untrue unless it is further assumed that the later ones are of greater mass or were stimulated to begin the differentiation at a later time. The acceptance of either of the assumptions as a complete justification would lead to a condition that does not seem biologically plausible, since it would suppose that in any group of cells, all possess precisely the same potentiality to undergo transformation. To a certain extent it is possible to avoid this difficulty by assuming that one can deal with an average b for the entire population of cells, admitting the possibility for variation of this parameter from individual to individual within the group. This particular approach will be adopted in the present discussion, as it proves to be a reasonable one. The further detailed analysis in terms of a distribution function for the b values is more complicated and will be reserved for a future study.

The assumption of an average b does not, however, solve the problem. There remains a difficulty of a peculiarly biological nature. From the constancy of b with time one must conclude that the differentiation of some portion of the group of cells has no apparent effect on the potentiality of the remaining undifferentiated ones. This is biologically unsound, for it in essence implies that each cell is physiologically isolated from the other members of the group as far as differentiation is concerned.

As has already been indicated in the general discussion of physiological competition, there are at least two ways in which the cells which have differentiated can influence the differentiation potentials of the remaining n-cells. Firstly, if the differentiation results in a change of metabolism, the new metabolites formed may prove harmful to the n-type cells and inhibit their transformation. Secondly, by their transformation they have decreased the amount of substrate available to the untransformed cells. Consequently, unless the available biological space and the rate of supply of the substrate are both above the critically limiting level, the appearance of each r-type cell results in a decrease of the differentiation potentials of the n-cells yet in existance.

If either or both of these two competitive inhibitory processes are operating, then, at any given stage of the transformation, it is necessary to decrease the inherent differentiation potentials of

the n-cells present, by an amount proportional to the mass of r-cells formed in the past. There exist no exact criteria by means of which the precise quantitative law of this variation can be decided upon. All that is known is that it must express potential limitation as a function of R, the mass of r-type that has appeared. For the purposes of the present discussion, it is sufficient to examine a simple linear relationship. We may then write for the "actual potential," (b_t), of the n-type cells at any given moment the following expression:

$$b_t = b - \lambda R, \qquad (7)$$

where λ is a constant and b denotes the inherent differentiation potential. Equation (7) may be considered as a first approximation of a more general expression containing the higher powers of R. It will be noted that at the beginning of the process, when R is small, the actual differentiation potential, b_t, approximates b. As the differentiation proceeds, however, and R gets larger, b_t gets smaller and smaller until it finally approaches zero when R becomes equal to $\frac{b}{\lambda}$. It is thus apparent that b_t is a differentiation potential that varies from moment to moment, since it is a function of R which in turn is a function of time.

From equation (7) it is apparent that the larger λ is, the greater is the inhibition of the potential by a given mass of the r-type. Thus, both from the method of its insertion and from its definition, λ is seen to be a measure of the effect of the transformation process on those cells of a group which have as yet not undergone differentiation. It may, therefore, properly be called the "coefficient of interaction."

It will be noted that both types of interaction, competition for substrate as well as for physiological space, have been combined into the single interaction coefficient, λ. From its nature it is evident that λ will vary inversely both with the volume of physiologically available space as well as with the rate of substrate supply. Insofar as its value is dependent on the direct competition for substrate, it is possible to deduce on physiological grounds the probable relation between λ and b.

At any given substrate level, the b value of a particular cell will depend on the ability, in terms of amount per unit of time, of the cell to use the substrate. This ability, or b value, may then be referred to the concentration of the enzymatic components which use the substrate and supply the necessary energy for the transformation. Thus, the higher the b value of a cell, the greater its content of the necessary enzymes. Whenever effective competition for substrate is occurring it is necessarily true that substrate concentration is the limiting factor governing the rate of transformation. Under these conditions the rate is determined by the product of the substrate and enzyme concentrations, i.e., T, the rate of transformation is given by

$$T = kES$$

where E and S represent enzyme and substrate concentrations respectively, and k is a proportionality constant. It is clear from the above relation that a cell with a high b value, corresponding to a high value for E, will be able to maintain a given rate of transformation at a lesser substrate concentration than a cell with a low b value. Consequently, as competition sets in, and the substrate concentration level begins to drop, the cells with the low differentiation potentials will be the most drastically affected. Further, if as seems reasonable, a minimal rate of energy supply is required for building up the necessary structures, the low b-value cells will be the first to cease active differentiation. On this basis it is necessary to conclude, then, that a general inverse relation exists between the inherent differentiation potential and the interaction coefficient of any particular cell, i.e., the higher the b, the lower the λ and vice versa.

A word may be interposed here about the relation between b_t and b, the inherent differentiation potential. b_t was introduced to approximate more closely experimental experience than was possible with a time-independent potential. However, it is not to be considered as a mere replacement of one expression by another more closely descriptive of the truth. The concept underlying b must still remain as part of the theory. The reason for this resides in the desirability of retaining some method for arriving at a measure of the intrinsic potentiality of the tissue, independent of environmental variation. The parameter b fulfills this function since it measures transformation capabilities in the complete absence of external limitations, whether they stem from the presence of other cells undergoing the same process in the neighborhood or from some unfavorable environmental element of a more inanimate nature. The reten-

tion of b as an environmental independent constant does not ignore external effects. On the contrary it permits their examination apart from the kinetic consequences of inherent variations in b. Unless a separation of this kind were made, it would be difficult to examine the consequences of gradients in b as distinct from the effect of environmental polarizations.

TRANSFORMATION KINETICS OF A PHYSIOLOGICALLY ISOLATED GROUP, THE MEMBERS OF WHICH ARE IN PHYSIOLOGICAL COMPETITION

The critical examination of the condition with complete absence of internal and environmental interaction permits a natural extension of the analysis to the case where some of the biologically implausible restrictions are removed. In particular, it is now possible to analyze the situation where:

1) Interaction obtains amongst cells within a group so that the differentiation potential at any moment of any given cell is affected by the number of cells which have already undergone transformation.
2) Environmental influences may be felt on the process of differentiation through ϵ, the environmental coefficient of resistance.

While environmental influences are of great importance, if they are uniformly applied their results need not be crucial for final development. If they are polarized so that a particular region of the group is more drastically affected than others, the environment could under such circumstances impose its own polarity on the developing structure. Extremely low values of ϵ will also make the environmental influences critical, since they could thus numerically overshadow the internal parameters and consequently dominate the course of development.

To study the kinetics of the differentiation with both cellular and environmental interaction, equation (3) must be modified to include these factors. The differential equation expressing the time-rate of appearance of the r-type now takes the form

$$\frac{dR}{dt} = b_t(K - R) \tag{8}$$

where K is defined by equation (6) and b_t by equation (7). Substituting for b_t its definition as given, we obtain,

$$\frac{dR}{dt}(K - R)(b - \lambda R) \tag{9}$$

As in the analysis of the previous differential equation, of paramount interest is the state of the system when transformation ceases and no further changes occur in the value of R. Such a condition is described when $\frac{dR}{dt}$ assumes the value of zero. As can be seen from equation (9), there are two values of R which will satisfy this condition. They are given by

$$R = K \tag{10a}$$

and

$$R = \frac{b}{\lambda} \tag{10b}$$

The first value characterizes the non-interacting case, or at least the one where no effective interaction exists amongst the transforming cells. The second presumably applies when competition occurs during the transformation. It is apparent however, from the existence of the two possible values for R that a positive non-zero value for λ is not sufficient to guarantee interaction effects. In order for potency limitation to emerge from the competitive interaction, it is necessary to demonstrate that under these conditions R will approach a value less than K. It is clear, then, that a necessary condition for the existence of limitation is that $\frac{b}{\lambda}$ be less than K. It may now be demonstrated that this condition is also sufficient, by showing that under this assumption R approaches $\frac{b}{\lambda}$ rather than K.

Since it is proposed to study interaction effects, a positive non-zero value for λ is assumed in the following. Returning to equation (9), transposing and integrating the result leads to

$$\frac{1}{b - \lambda K} \ln \frac{\lambda R - b}{R - K} - \ln C_2 = t + C_1 \tag{11}$$

where C_1 and C_2 are constants of integration determined by initial and final conditions. Passing to natural numbers, we obtain from equation (11)

$$\frac{\lambda R - b}{R - K} = C_2 e^{(b - \lambda K)(t + C_1)} \tag{12}$$

Solving for R yields,

$$R = \frac{b}{\lambda - C_2 e^{(b - \lambda K)(t + C_1)}} - \frac{K C_2 e^{(b - \lambda K)(t + C_1)}}{\lambda - C_2 e^{(b - \lambda K)(t + C_1)}} \tag{13}$$

Equation (13) represents a complete description of the transformation of R as a function of time. It is now necessary to inquire what happens to R as t increases indefinitely under the particular assumption that $\frac{b}{\lambda}$ is less than K. It will be noted that this assumption implies that

$$b - \lambda K < 0$$

Consequently, when t is very large in equation (13), the exponentials having negative exponents become smaller, and with increasing t approach zero. The second term, possessing as it does an exponential in the numerator, disappears completely. Of the first term only b and λ remain. Thus the

$$\lim_{t \to \infty} R = \frac{b}{\lambda} \tag{14}$$

which, since $\frac{b}{\lambda}$ is less than K, signifies interaction leading to potency limitation. It is then possible to state the following general theorem on transformation dynamics.

Theorem 1. The necessary and sufficient conditions that a group of transforming cells fails to realize its full potentiality for differentiation are that its members be in physiological competition and that the coefficient of interaction λ be greater than $\frac{b}{K}$.

It is of some interest to investigate what the theory predicts for the time independent value of R if $\frac{b}{\lambda}$ is greater than K, i.e., would R still approach $\frac{b}{\lambda}$? Under this assumption

$$b - \lambda K > 0$$

and the coefficients of t in the exponents are all positive. The limit approached by R for increasing time in this case may perhaps be more readily seen if equation (13) is rewritten as

$$R = \frac{\frac{\lambda}{e^{(b-\lambda K)(t+C_1)}}}{\frac{\lambda}{e^{(b-\lambda K)(t+C_1)}} - C_2} - \frac{KC_2}{\frac{\lambda}{e^{(b-\lambda K)(t+C_1)}} - C_2} \tag{15}$$

Here it is observed that with increasing t, the first term of the right hand member disappears, since its numerator goes to zero, and the second term reduces to K after cancellation of C_2. Thus, we find

$$\lim_{t \to \infty} R = K$$

The results obtained on the consequences of the two inequalities may be summarized in the following two statements

1. If $\frac{b}{\lambda} < K$, $\quad \lim_{t \to \infty} R = \frac{b}{\lambda}$

2. If $\frac{b}{\lambda} > K$, $\quad \lim_{t \to \infty} R = K$

It is of interest to note here for later use that the same conclusions may be derived directly from the differential equation (9) under the assumption that $\frac{dR}{dt} \leqq 0$. If $\frac{b}{\lambda} < K$, then R cannot become greater than $\frac{b}{\lambda}$ for then $\frac{dR}{dt} < 0$. If $\frac{b}{\lambda} > K$, then R cannot exceed K for then again $\frac{dR}{dt} < 0$. Hence statements 1 and 2 follow.

It is thus seen that when two values of R exist which will make $\frac{dR}{dt}$ vanish, the value which is actually assumed in the steady state is always the lesser of the two. This is merely another way of stating that limitation effects must occur if the interaction is sufficiently severe to insure that λ is large enough to make the ratio $\frac{b}{\lambda}$ less than K.

It is not necessary for the main problem to pursue the examination of the characteristics of the isolated group any further. With the emergence of potency limitation as a consequence of inter-member competition, the analysis has been brought to the point where an extension can be made which will permit an inquiry into the questions of group interaction and its effects.

Group Interaction

In harmony with the analysis as it has proceeded thus far, we may state the central problems of group interaction in the form of the following questions:

1) How, in general, is the physiologically isolated case changed when the group is placed in physiological contact with another undergoing the same transformation?
2) Under what conditions will potency limitation emerge from the group interaction?
3) What role do gradients in 'physiological activity' play in the transformation kinetics of such connected groups?

The first question poses the primary problem whose solution is essential before the others can

be answered. In essence it asks, how must the kinetic equation of a group be modified when it is physiologically connected with another one. To make the problem more concrete, consider the case of two masses of tissue, each capable of differentiating into the same structure when isolated. Let one be of mass M_1, with a differentiation potential b_1, interaction coefficient of λ_{11}, and a coefficient of environmental resistance e_1. Similarly, the parameters describing the second group may be denoted by M_2, b_2, λ_{22}, and e_2 respectively. If the two groups are unconnected, then for each may be written a differential equation similar to equation (9). We would then write

$$\frac{dR_1}{dt} = (K_1 - R_1)(b_1 - \lambda_{11} R_1) \qquad (16a)$$

$$\frac{dR_2}{dt} = (K_2 - R_2)(b_2 - \lambda_{22} R_2) \qquad (16b)$$

where as before,

$$K_1 = e_1 M_1$$

and

$$K_2 = e_2 M_2$$

Since it is desired to examine interaction effects it will be assumed in the following discussion that λ_{11} and λ_{22} are both greater than zero and further that $\frac{b_1}{\lambda_{11}}$ is less than K_1 and $\frac{b_2}{\lambda_{22}}$ is less than K_2. Under these assumptions, the steady state values of R_1 and R_2 will be determined by the second of the two factors in the right-hand members of equations (16a) and (16b).

It was earlier suggested that gradients were necessary but not sufficient conditions for the existence of regulatory behavior. This proposition is of such crucial importance to the whole problem of the implementation of gradients as directive agents in morphogenesis, that a more rigorous re-examination of the problem is desirable. This may be done with the aid of equations (16a) and (16b). For the purposes of discussion let us assume that the two groups described by these equations belong to the same animal, group 1 being anterior to group 2. Furthermore, a gradient in 'physiological activity' exists such that it decreases posteriorly, being highest at the most anterior end of the animal. This physiological activity, insofar as it refers to differentiation activity, may best be measured by b, the inherent differentiation potential. With above assumptions, then, b_1 is greater than b_2.

We may now ask whether the existence of this gradient in b has any consequences for the kinetics of the transformations in the two groups, as described by equations (16a) and (16b). To put the problem in more specific terms, we may inquire whether the activity of the more anterior group affects through suppression or otherwise the differentiation of the posterior one. The answer is of course in the negative. This is not surprising, since no condition of connectivity has been imposed on these equations. They are completely independent, and consequently each has a solution of the form given by equation (13). The complete suppression of the activity of group 1, so that $\frac{dR_1}{dt}$ would assume a value of zero throughout the period of observation, would have no effect on either the existence of a limiting value for R_2, nor the magnitude of this value. It is solely determined by the ratio $\frac{b_2}{\lambda_{22}}$ and contains none of the parameters or variables which describe the condition and kinetics of group 1. Similarly, nothing going on in group 2 could possibly exert any influence on the transformation of group 1. It can be logically deduced, then, that the existence of a potential gradient does not unequivocally imply dominance over or suppression of one group by the more active one.

As was stated earlier, if it is desired that the two groups interact, the crux of the problem will lie in the mechanism assumed for the interaction. Mathematically, it is necessary to replace the set of independent differential equations by a system of such equations, not all of which possess solutions independent of the others. There are many ways in which this can be accomplished. In general, it is sufficient that the equation of each group contain some function of the variable R of the other group (or groups) with which it is interacting. The particular function chosen will depend on the biological mechanism selected for the interaction. Examination of the biology of the situation makes the problem of choice a relatively simple one.

Essentially, physiological connectivity or interaction would imply that the production of an r-type cell in one group should somehow influence the ability of the n-type cells in the connected group to undergo differentiation. It will be recalled that in correcting the condition of rigid physiological isolation of the member cells within a group, essentially the same problem was encountered on a lower biological level. The isolation was removed by assuming that the production of every r-cell decreased the differentiation potential

of all the remaining n-cells; this decrease being interpreted in terms of substrate utilization as well as the production of harmful metabolites, or in general physiological competition. It is readily seen that an extension of this type of interaction amongst cells within a group to one involving cells of different groups provides a simple mechanism for group interaction. It is certainly reasonable to suppose that two groups of cells, each differentiating into the same structure, producing the same metabolites, and drawing on the same substrate source would influence each other in the same general way as do two member cells of a group. This would necessitate the existence of some physical connection between the groups. Among other means this could be accomplished through a circulatory medium from which both groups could draw on the same supply of substrate and into which they could both pour their metabolic wastes. If this physical linkage condition is satisfied, then the production of an r-cell in either group would decrease the potential of all the n-cells, in both of them. In terms of the variables and parameter thus far employed, this would mean that every increase in R_1 would decrease not only b_1 but also b_2. Similarly, every increase in R_2 would decrease the inherent potentials of both groups. Under these circumstances the actual differentiation potentials for the two interacting groups will be given by

$$b_{t_1} = b_1 - \lambda_{11}R_1 - \lambda_{12}R_2 \qquad (17)$$

for group 1 and by

$$b_{t_2} = b_2 - \lambda_{22}R_2 - \lambda_{21}R_1 \qquad (18)$$

for group 2, where λ_{11} and λ_{22} have their previous significance, and λ_{12} measures the effect on the differentiation potential of group 1 of the production of r-type cells in group 2. λ_{21}, on the other hand, measures the effect on the differentiation potential of group 2 of the production of r-type cells in group 1. Both λ_{12} and λ_{21} may then be called the coefficients of *group interaction*. The differential equations describing the transformation kinetics of the two connected groups 1 and 2 than take the forms,

$$\frac{dR_1}{dt} = (K_1 - R_1)[(b_1 - \lambda_{12}R_2) - \lambda_{11}R_1] \qquad (19)$$

for group 1, and

$$\frac{dR_2}{dt} = (K_2 - R_2)[(b_2 - \lambda_{21}R_1) - \lambda_{22}R_2] \qquad (20)$$

for group 2.

Fundamentally, it is of interest to examine whether potency limitation due to group interaction is inherent in these equations. Ultimately it would be desirable to determine whether dominance of one group over the other is also a deducible consequence. To aid in the analysis of equations (19) and (20) the following assumptions are made:

(1) $\lambda_{12} > 0, \lambda_{21} > 0, b_1 > 0, b_2 > 0, \lambda_{11} > 0, \lambda_{22} > 0$

(2) $\bar{R}_1 > 0, \bar{R}_2 > 0$

(3) $\frac{b_1}{\lambda_{11}} < K_1, \frac{b_2}{\lambda_{22}} < K_2$

(4) $\frac{dR_1}{dt} \geqq 0; \frac{dR_2}{dt} \geqq 0$

Assumptions (1) and (2) insure group interaction effects; the former guaranteeing physiological connectivity, the latter differentiation activity in both groups. Assumption (3) allows equations (19) and (20) to reduce to the physiologically isolated case with effective intermember competition within each group when the two coefficients of group interaction, λ_{12} and λ_{21}, are both equal to zero. Assumption (4) implies that no net decrease occurs in the number of the r-type cells in either group, i.e., dedifferentiation does not occur. This last assumption also permits the use of the argument in small type on page 128 to determine the steady state values of R_1 and R_2; thus the analysis may be made with the differential equations.

As in previous cases the end point of the transformation in a particular group will be reached when its R attains a value which will make its $\frac{dR}{dt}$ vanish. Under the assumptions on equations (19) and (20) it is clear that the steady state values for R_1 and R_2 will be obtained by setting the second of the two factors in the right-hand members of equations (19) and (20) equal to zero. Denoting the steady state values of R_1 and R_2 by $\bar{R}_1$ and $\bar{R}_2$ respectively, we thus have

$$b_1 - \lambda_{12}\bar{R}_2 - \lambda_{11}\bar{R}_1 = 0 \qquad (21)$$

$$b_2 - \lambda_{21}\bar{R}_1 - \lambda_{22}\bar{R}_2 = 0 \qquad (22)$$

Limited Realization as a Consequence of Group Interaction

That potency limitation is an immediate consequence of group interaction may be directly de-

duced from equations (21) and (22). Solving for $\bar{R}_1$ in equation (22) we find

$$\bar{R}_1 = \frac{b_1}{\lambda_{11}} - \frac{\lambda_{12}\bar{R}_2}{\lambda_{11}} \tag{23}$$

Since λ_{11}, λ_{12}, and $\bar{R}_2$ are all greater than zero, it follows that $\bar{R}_1$, the steady state value attained when the groups are connected, is less than $\frac{b_1}{\lambda_{11}}$, the steady state value reached by group 1 in isolation, i.e., for $\lambda_{12} = 0$. Similarly for group 2, it is found from equation (22) that

$$R_2 = \frac{b_2}{\lambda_{22}} - \frac{\lambda_{21}\bar{R}_1}{\lambda_{22}} \tag{24}$$

Here again, since $\bar{R}_2$ is less than $\frac{b_2}{\lambda_{22}}$, potency limitation due to physiological connectivity of the two groups is exhibited.

Dominance and Gradients

In order to examine the question of dominance and the effect of gradients on the transformation kinetics of connected groups it is necessary to determine what relation $\bar{R}_1$ bears to $\bar{R}_2$. Thus, for example, should $\bar{R}_1$ prove to be greater than $\bar{R}_2$, one could conclude that group 1 is dominant to group 2. Whereas, if the inequality were reversed, it would follow that dominance relations are also reversed. An examination of the desired nature may be made by solving equations (21) and (22) for $\bar{R}_1$ and $\bar{R}_2$ in terms of the parameters. The solutions thus obtained for $\bar{R}_1$ and $\bar{R}_2$ are given by

$$\bar{R}_1 = \frac{\lambda_{22}b_1 - \lambda_{12}b_2}{\lambda_{22}\lambda_{11} - \lambda_{12}\lambda_{21}} \tag{25}$$

$$\bar{R}_2 = \frac{\lambda_{11}b_2 - \lambda_{21}b_1}{\lambda_{22}\lambda_{11} - \lambda_{12}\lambda_{21}} \tag{26}$$

It may be noted as a check on these last two equations that they correctly predict values characteristic of the non-interacting case for zero values of corresponding group interaction coefficients; i.e., when λ_{12} is taken as zero, $\bar{R}_1$ reduces to $\frac{b_1}{\lambda_{11}}$, whereas if λ_{21} is taken to be equal to zero, $\bar{R}_2$ reduces to $\frac{b_2}{\lambda_{22}}$. Both $\bar{R}_1$ and $\bar{R}_2$ involve all the coefficients of interaction as well as both differentiation potentials. It is clear, then, that several quite different situations may obtain as far as their relative values are concerned. Any difference which may exist between $\bar{R}_1$ and $\bar{R}_2$ may equally likely depend on their potentials, interaction coefficients, group interaction coefficients, or a combination of these parameters. The major interest of the present discussion demands an analysis of those conditions which are necessary and sufficient for dominance. It is consequently desirable to examine the above possibilities separately insofar as such an examination is feasible. A comparison of the relative magnitudes of $\bar{R}_1$ and $\bar{R}_2$ can be more readily made if equations (25) and (26) are rewritten as

$$\bar{R}_1 = \frac{b_1(\lambda_{22} + \lambda_{21})}{\alpha} - \frac{\beta}{\alpha} \tag{27}$$

$$\bar{R}_2 = \frac{b_2(\lambda_{11} + \lambda_{12})}{\alpha} - \frac{\beta}{\alpha} \tag{28}$$

where,

$$\alpha = \lambda_{22}\lambda_{11} - \lambda_{12}\lambda_{21}$$

and

$$\beta = \lambda_{21}b_1 - \lambda_{12}b_2.$$

It is evident from equations (27) and (28) that since all other terms and factors are the same, attention need be focused in the following only on the numerators of the first terms of the right-hand members.

Case 1. *Absence of Gradients in Interaction Coefficients.*

In this case, emphasis is placed on the consequences for the transformation of the various possible order relations between the b values. It is assumed that λ_{11} equals λ_{22} and λ_{12} equals λ_{21}. Under these assumptions, it is evident from equations (27) and (28) that the following statements are true:

1. If $b_1 > b_2$, then $\bar{R}_1 > \bar{R}_2$;
2. If $b_1 < b_2$, then $\bar{R}_1 < \bar{R}_2$;
3. If $b_1 = b_2$, then $\bar{R}_1 = \bar{R}_2$.

It is thus seen that dominance is a consequence of gradients in potential, absence of a gradient leading to the disappearance of dominance relations. The theory further specifies the direction in which dominance will occur. The above inequalities indicate that under the conditions being considered, the group with the higher potential will dominate the other.

Case 2. *Absence of Gradients in Differentiation Potentials.*

Here b_1 is assumed to be equal to b_2. Since the interaction coefficients and group interaction coefficients stem from the same physiological mechanism, these two parameters of any given group may be allowed to vary in the same direction. Thus we assume that if $\lambda_{11} < \lambda_{22}$, then $\lambda_{12} < \lambda_{21}$. This seems reasonable, since if, e.g., members of group 1 are affected less by the formation of an r-type cell than are members of group 2, the particular position occupied by the r-type cells should not reverse the order relation between the coefficients. While this assumption of direct relation between the two types of interaction coefficients is not necessary for the mathematical analysis, it is a useful one for several reasons. In the first place, such a relation is physiologically more plausible than complete independence. Secondly, the examination of all the possible permutations of the order relations between the four coefficients which a supposition of independence would necessitate hardly seems profitable at the present stage. The following statements may then be written with the aid of equations (27) and (28):

1. If $(\lambda_{22} + \lambda_{21}) > (\lambda_{11} + \lambda_{12})$, then $\bar{R}_1 > \bar{R}_2$;
2. If $(\lambda_{22} + \lambda_{21}) < (\lambda_{11} + \lambda_{12})$, then $\bar{R}_1 < \bar{R}_2$;
3. If $(\lambda_{22} + \lambda_{21}) = (\lambda_{11} + \lambda_{12})$, then $\bar{R}_1 = \bar{R}_2$.

Here again, dominance emerges as a result of a gradient. As is to be expected from the nature of the parameters, the dominant group in this case is the one which possesses the lower valued coefficients of interaction.

The third possibility, where no inequalities exist either between the differentiation potentials or the interaction coefficient, needs no detailed discussion, since it is clear from statements 3 of both cases that this leads immediately to equality between $\bar{R}_1$ and $\bar{R}_2$, i.e., absence of dominance.

The statements listed under cases 1 and 2 demonstrate that a gradient in physiological activity whether it be measured in terms of the potentials or interaction coefficients, is a *sufficient* condition for the existence of dominance. Is it a necessary condition? That is to say, does the existence of dominance phenomena necessarily imply the coexistence of gradients in physiological activity? This question has been raised several times in the literature of critical discussions of the relations between gradients and dominance. Within the confines of the present theory the answer is in the affirmative. To demonstrate this, it is sufficient to show that the order relations used as hypotheses may be deduced from the conclusions. Thus under case 1, it is clear from equations (27) and (28) that

1. If $\bar{R}_1 > \bar{R}_2$, then $b_1 > b_2$;
2. If $\bar{R}_1 < \bar{R}_2$, then $b_1 < b_2$;
3. If $\bar{R}_1 = \bar{R}_2$, then $b_1 = b_2$;

and under case 2 that

1. If $\bar{R}_1 > \bar{R}_2$, then $(\lambda_{22} + \lambda_{21}) > (\lambda_{11} + \lambda_{12})$;
2. If $\bar{R}_1 < \bar{R}_2$, then $(\lambda_{22} + \lambda_{21}) < (\lambda_{11} + \lambda_{12})$;
3. If $\bar{R}_1 = \bar{R}_2$, then $(\lambda_{22} + \lambda_{21}) = (\lambda_{11} + \lambda_{12})$.

Case 3. *Inverse Relation Between Gradients in Potentials and Interaction Coefficients*

The setting up of cases 1 and 2 as separate problems for analysis implies that the interaction coefficients may vary independently of the differentiation potentials. This situation is possible under certain special conditions, and it was thus of interest to examine the consequences of gradients in the interaction coefficients above. However, as was pointed out previously (see pp. 127–128), a physiological interpretation of the interaction coefficients would indicate the existence of an inverse relation between them and the group potentials. Symbolically this would mean that

(a) if $b_1 > b_2$, then $\lambda_{11} < \lambda_{22}$ and $\lambda_{12} < \lambda_{21}$;
(b) If $b_1 < b_2$, then $\lambda_{11} < \lambda_{22}$ and $\lambda_{12} > \lambda_{21}$;
(c) If $b_1 = b_1$, then $\lambda_{11} = \lambda_{22}$ and $\lambda_{12} = \lambda_{21}$.

With the aid of (a), (b), and (c), and equations (27) and (28), the following statements may be made:

(1) If $b_1 > b_2$, then $\bar{R}_1 > \bar{R}_1$;
(2) If $b_1 < b_2$, then $\bar{R}_1 < \bar{R}_2$;
(3) If $b_1 = b_2$, then $\bar{R}_1 = \bar{R}_2$.

Dominance thus follows as a consequence of gradients in b without further postulating any relations amonst the interaction coefficients, since they are fixed by the inverse relation they bear to the potential. This case thus confers, in addition to physiological plausibility, the advantage of being able to confine the discussion to one parameter. It is evident that in this case, as in the others, the existence of a gradient is not only a sufficient condition for dominance, but also a necessary one, since the following propositions are true:

(1) If $\bar{R}_1 > \bar{R}_2$, then $b_1 > b_2$;
(2) If $\bar{R}_1 < \bar{R}_2$, then $b_1 < b_2$;
(3) If $\bar{R}_1 = \bar{R}_2$, then $b_1 = b_2$.

The results of the present section may be sum-

marized in the following theorems on transformations dynamics.

Theorem 2. A transforming group physiologically connected to another group which is also actively differentiating will experience potency limitation.

Theorem 3. A sufficient condition for the absence of dominance phenomena between transforming groups is that the coefficients of group interaction be zero.

Assuming positive non-zero coefficients of group interaction, the following theorems on dominance may be stated.

Theorem 4. In the absence of gradients in interaction coefficients a necessary and sufficient condition for the existence of dominance is a gradient in differentiation potential; the group possessing the higher differentiation potential will dominate the other.

Theorem 5. In the absence of gradients in differentiation potentials, a necessary and sufficient condition for the existence of dominance is a gradient in interaction coefficients; the group possessing the lower interaction coefficients will dominate the other.

Case 3, upon which all subsequent discussion will be based, yields

Theorem 6. If the potential of any group is inversely proportional to its coefficients of interaction, then a necessary and sufficient condition for the existence of physiological dominance is that there be a gradient in differentiation potential. The dominating group is characterized by the highest potential.

EXPERIMENTAL INTERPRETATION OF THE COEFFICIENT OF GROUP INTERACTION

A positive value for $\lambda_{ij} (i \neq j)$, according to the particular mechanism chosen for group interaction, can only be assumed when there exists a physical connection between the two groups which would allow flow of material between them. Any experimental procedure that destroys this physical continuity would result in a zero value for λ_{ij} and hence in physiological isolation for group i. If group i were a low potential group, this would necessarily be followed by the disappearance of any regulative action by the dominant group over the now isolated region. On the other hand, if group i were itself the dominant group, its isolation would release the others to which it was connected from its inhibitory influence. Such isolation can be experimentally attained most obviously by sectioning, incisions, constrictions, or blocking a circulatory system if one exists.

There is, however, another method of attaining isolation which is inherent in the basic concept of physiological competition. The coefficients of group interaction stem from the same resistances to transformation as do the ordinary interaction coefficients. They will vary inversely as the physiologically available space, insofar as competition for biological space contributes to their value. The widespread ability of cells which do not normally transform, to differentiate in isolation, would presuppose that most, if not all, produce the required substrate. It must be concluded, then, that the amount physically available to any group is directly proportional to the total volume or mass of cells physiologically connected to it. The severity of the competition between the two groups should then depend on the total mass of tissues with which they have established connection. Thus, insofar as direct competition for substrate contributes to the value of λ_{ij}, the coefficient of group interaction, it will again vary inversely as the total volume of tissue connected to the competing groups. Consequently, if a sufficient volume were so connected, λ_{ij} could effectively be made zero, and the two groups could be spoken of as in physiological isolation.

This particular interpretation of λ_{ij} has certain well defined implications for the experimental attack on the problem of dominance, to which we shall return when we consider that phenomenon in the regeneration of hydranths in coelenterates.

The type of physical connection established for mass transport between two competing groups is of some importance in determining the magnitude of the coefficient of group interaction, whether direct or indirect competition or both are involved. An effective circulatory system will tend to decrease local autonomy and increase the coefficient of interaction between groups. The complete absence of a circulatory system, with a consequent dependence upon the limited effectiveness of diffusion, will weaken regulative activity stemming from this mechanism. Even relatively small separations may in this case lead to more or less complete physiological isolation of two groups.

PHYSIOLOGICAL DOMINANCE

The primary purpose behind the development of the theory was to see if, on the basis of a simple

mechanism, the regulatory nature of normal morphogenesis could be logically deduced. To some extent the analysis has already achieved this goal. However, thus far in the discussion of dominance, reference has been made only to its presence or absence. It would be highly desirable if the theory were to permit a more quantitative examination of dominance phenomena. Unfortunately, too many experimental and theoretical problems remain unsolved for a completely satisfactory quantitative approach to be developed at present. However, it is possible to derive certain interesting relations which have the advantage of being comparable with data on hydroid regeneration and thus offer an opportunity for testing the adequacy of the theory.

It is evident that a quantitative definition of physiological dominance must involve the severity of the inhibition of the less active group. The extent of the suppression is basically determined by the steepness of the gradients in differentiation potentials as well as by the magnitudes of the coefficients of group interaction.

A semi-quantitative approach to the problem may be made from the fundamental equations for the actual differentiation potentials of two groups, i and j, in competition with each other. These are given by

$$b_{i_i} = [(b_i - \lambda_{ij}R_j) - \lambda_{ii}R_i] \tag{29}$$

$$b_{i_j} = [(b_j - \lambda_{ji}R_i) - \lambda_{jj}R_j] \tag{30}$$

Assuming that b_i is greater than b_j, the severity of the suppression or regulation of the transformation of the j-group by group i, reduces to the question of how soon b_{ij} will reach a value of zero.

It is manifest that several different situations can arise here. If both groups start their transformations simultaneously, and both have a zero value for their respective R, then a complete suppression of the inhibited group cannot occur, in a mathematical sense at least. During some finite period of time, R_f must assume a finite positive value. From a practical point of view, however, if the value be small enough, it need not be detectable, and a zero value may be assigned to it This hidden kind of differentiation cannot in all cases be ignored. Especially is this true in experiments involving the measurement of the differentiation rates of inhibited regions after their release from the regulation of dominant groups by isolation procedures. It is possible that the acceleration sometimes observed in these experiments is only apparent and is made up in part, at least, of the early unobservable portions of the transformation.

Complete suppression can of course occur if at the outset of the transformation of the J-group, group i has already reached some value R_i such that

$$(b_j - \lambda_{ji}R_i) = 0 \tag{31}$$

for if this be the case no r-type cells could form in group-j.

It is extremely interesting to examine the extent of the limitation experienced by a dominated group. Consider again two groups i and j competitively interacting, with group i being the dominating one. The steady state values attained by the two groups are given by

$$\bar{R}_i = \frac{b_i}{\lambda_{ii}} - \frac{\lambda_{ij}\bar{R}_j}{\lambda_{ii}} \tag{32}$$

$$\bar{R}_j = \frac{b_j}{\lambda_{jj}} - \frac{\lambda_{ji}\bar{R}_i}{\lambda_{jj}} \tag{33}$$

The extent of the limitation resulting from the interaction may be obtained from the difference between the above steady state values and those attained in physiological isolation, i.e., $\frac{b_i}{\lambda_{ii}}$ for group i and $\frac{b_j}{\lambda_{jj}}$ for group j. These differences are gives by

$$\overline{\Delta R_i} = \frac{\lambda_{ij}\bar{R}_j}{\lambda_{ii}} \tag{34}$$

$$\overline{\Delta R_j} = \frac{\lambda_{ji}\bar{R}_i}{\lambda_{jj}} \tag{35}$$

These last two equations demonstrate one of the most important characteristics possessed by the present formulation, viz., a direct relation between the potency limitations of the inhibited group and the differentiation level arrived at by the dominant one. Several interesting and experimentally valuable consequences are immediately deducible. In the first place, it would imply that the closer group i is to the completion of its transformation, the stronger is its regulative activity. Furthermore, it would predict that when the complete structure is finally formed, the severity of the inhibition of the j-group will be greatest, for then R_i has attained its maximum value. The significance of this prediction lies not only in the fact that it presumes a regulatory

activity for complete structures, but perhaps even more important, provides a simple and concretely specified mechanism through which such structures can control transformation activity in other parts of an organism, though they themselves are not apparently engaged in active differentiation.

The prediction of maximal regulatory intensity from fully transformed groups would imply certain well defined *time relations* for the dominance intensity between competing groups. For example, suppose group i is stimulated to begin its differentiation first, and after a certain interval of time group j is started. Under these circumstances, group j, instead of beginning its transformation with a differentiation potential of b_j, possesses one decreased by $\lambda_{ji}R_i$ where R_i is the value arrived at by the i-group during the interval of delay. If the latter is sufficiently great, the j-group will not get very far along the path toward the formation of a finished structure. We may thus have a situation where the inhibited group would have a much severer limitation on its potency realization than if it were started at the same time as the dominant group.

The theory would thus demand a dependence of dominance intensity on the time relations between the developmental processes of connected groups, and particularly on the interval between the stimulations to activity. In general, the longer the period of delay to the stimulation of the less active group, the more intense will the dominance be. It is clear that a reversal of the time relations should lead not only to a diminution of the regulative severity of the lower potential group, but in addition, should result in its final disappearance, if the interval of delay were of sufficient length. Under favorable circumstances, provided the discrepancy between the b-values were not too great, a complete reversal of dominance relations should be thus obtainable.

An opportunity to test these as well as other conclusions is afforded by the data on hydranth regeneration which is considered in the following section.

APPLICATION OF THE THEORY OF COMPETITIVE INTERACTION TO THE PROBLEM OF HYDRANTH RECONSTITUTION IN COELENTERATES

The very early work by Driesch (1897), Child (1907), Morgan (1903), and others on hydranth reconstitution clearly revealed that there could be no question of either predetermined regions destined to form particular structures, nor of a fixed polarity. Their experiments demonstrated concisely and unequivocally that any level of the hydroid stem has the ability to regenerate a hydranth. Recent work on the same question (see, e.g., Child, 1929, 1932; Zwilling, 1941) has served to emphasize this basic finding. Equally clear, however, is the fact that under the conditions of normal development, only the apical or distal end produces this structure, the potentialities of the more proximal portions being suppressed.

As far as regulatory activity is concerned, it is sufficient for the applicability of the competition theory to any particular case that two conditions be satisfied: first, physiological connectivity; second, the existence of gradients in ability to differentiate. With reference to the first, it would be difficult to deny the existence of physiological interaction between two regions connected physically to a common coelenteron containing a circulatory medium. In connection with the second condition, it is interesting to note that graded difference in rates of differentiation were pointed out by both Driesch and Child in the early work cited. More recently, Barth (1938) made a quantitative study showing how the rate of regeneration varies with the level of the stem. A typical set of measurements are reproduced in Fig. 1. In these experiments the rates of differentiation were so measured that they give an estimate of mass transformed per unit of time. Care was also taken to avoid interaction between regions during the measurement, so that the inherent rate of each level was obtained. The values can be associated with b, the inherent differentiation potential of the theory. The data demonstrate clearly that a real gradient exists in the ability to differentiate as measured by the rate of differentiation.

(*A*) *Experimental Conditions Leading to the Disappearance of Dominance*

A fruitful approach to the comparison of theory with experiment may be employed by noting whether the experimental conditions leading to the disappearance of regulation correspond to those deducible from the formulation.

In this connection we may examine certain experimental findings which when considered together present a more or less critical interpretive problem. *Tubularia* stems of intermediate length (from 5 to 10 mm.) display the familiar regulative behavior of the distal end over proximal reconstitution. However, short stems of about 1 mm.

in length do not show such distal dominance. Furthermore, the distal ends of stems 15 or more millimeters in length also lose their ability to control the differentiation of the proximal ends.

The loss of distal dominance in the two rather different experimental conditions cited above may be explained from the point of view of a competitive interaction between the two ends. In any potential gradient if any two points are taken sufficiently close together, the difference between them can be made vanishingly small. Thus the distal end of a short stem would lose its ability to regulate the regeneration at a proximal end simply

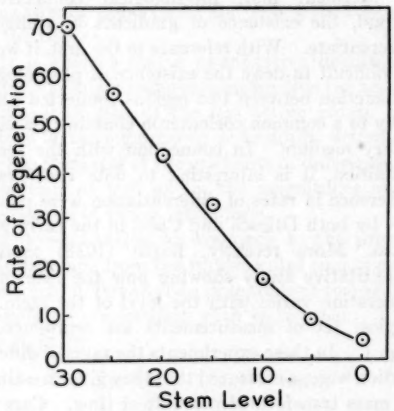

FIG. 1. RATES OF REGENERATION AT DIFFERENT LEVELS OF THE STEM OF TUBULARIA

Stems 30 mm. in length cut into 6 pieces and ligatured in the middle. Each point is the average of 10 stems. R_2 calculated by means of $\frac{\pi r^2 L}{t}$ where r is the radius of the stem cross-section, L is the length of the primordium, and t is the time in hours between cutting and the formation of the primordium. Zero mm. is at the proximal end of the stem, 30 mm. is at the distal end. (After Barth, 1938.)

because one of the necessary conditions for dominance, i.e., an effective gradient in differentiation potential, no longer obtains between the two groups. The discussion of the characteristics of λ_{ij}, the coefficient of group interaction, permits a relatively simple interpretation of the disappearance of dominance in the experiments with long stems. The physiologically connected volume, with which λ_{ij} varies inversely, has been made so large that these interaction coefficients have disappeared from the kinetic equations, at least insofar as they critically determine the end point in the transformations of the two groups.

The further examination of the concept of physiological connectivity as it applies to the particular organism in question leads to other interesting experimental methods for abolishing dominance. The essential condition of connectivity, implying as it does mass transport, must depend on a free access of the coelenteronic fluid from one group to the other. Thus, any interference with the free circulation of this fluid should lead to a parallel loss in the ability of the distal end to inhibit hydranth formation in the proximal portion of the stem. Such experiments have been done (Barth, 1938), blocking of the material exchange being produced by means of a ligature between the two ends. As is well known, treatment of this kind is invariably accompanied by a loss of regulatory activity in stems which would normally show it.

Experiments which use ligatures to obtain isolation of the distal and proximal halves are open to the obvious criticism that the procedure prevents not only the flow of fluid, but since the ligatures cut through the coenosarc, the transmission of stimuli is also hindered. To avoid this situation, prevention of material transport in the experiments of Barth (1938) and Rose and Rose (1941) was obtained by the injection into the coelenteron of either an oil drop or an oxygen bubble of sufficient size to stop fluid flow. The same disappearance of dominance relations was obtained in these experiments.

(*B*) *Experimental Modification of Transformation Kinetics*

An examination of the kinetic equations 19 and 20 for two competing regions shows that isolation (i.e., making λ_{12} and λ_{21} zero) should be followed by an increase in the rate of transformation. Data of this nature have been obtained by Barth (1938) for the coelenterate *Tubularia*. Rate was measured in terms of volume of hydranth formed divided by the time taken to arrive at a constriction between the primordium and the rest of the stem.

In choosing the experimental procedure to make the $\lambda_{12}R_2$ and $\lambda_{21}R_1$ terms disappear from the equations, it is important to avoid changing other factors than that of intergroup competition. Thus a ligature placed so as to divide the stem in two parts as shown in (b) of Fig. 2 effectively removes the possibility of distal-proximal competition, and consequently reduces both λ_{12} and λ_{21} to zero. However, at the same time the physiological space available to both groups is drastically decreased,

resulting in proportionate increases in the coefficients of internal interaction, λ_{11} and λ_{22}. The net effect as far as resultant rates are concerned would under such circumstances be difficult to predict, since even decreases in rate might be obtained if isolation is produced in this manner. Indeed, such decreases would be expected providing the comparison is made with a very long stem in which all interaction coefficients are near zero, with the same kind of stems when the physiological space of each group is halved by a middle ligature. In an actual experiment in which 25 mm. stems were used, a ligature in the middle produced a 36 per cent decrease in the transformation rate of the distal half and about a 20 per cent decrease in that of the proximal.

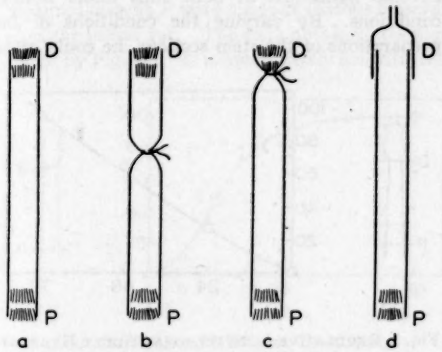

FIG. 2. EXPERIMENTAL CONDITIONS

P and D refer to proximal and distal ends respectively.
(a) Distal and proximal ends in competition;
(b) Isolation of the two ends (D, P) with a concomitant change in physiological space available to each;
(c) Isolation of the two ends (D, P) with little if any change in physiological space available to the proximal group;
(d) Isolation of proximal end obtained by inhibiting differentiation in distal end.

Focussing attention on the proximal group, which will be designated as group 2, a more adequate experiment would be to compare the rate of hydranth formation at the proximal end of (a) in Fig. 2 with that of the proximal end of (c) in the same figure. Here removal of the competition with the distal end is not accompanied by any significant changes in the physiological space available to the proximal portion of the stem. As can be seen from Table 1, experiments performed in this manner show a uniform increase in the transformation rates of the proximal ends over those obtained when the latter are in competition with the distal regions.

It will be noted that the method of ligaturing used in these experiments made the λ_{21} zero and thus removed the interaction term, $\lambda_{21}R_1$ from the rate equation. It is clear that another way of accomplishing the same thing would be to make and keep the R_1 zero, leaving physiological connectivity intact. As far as the quantitative effect on rate is concerned, the theory would predict that the same general increase would be obtained. Restriction of R_1 to a zero value can be accomplished by inhibiting regeneration at the distal end by means of a glass tube placed over it, as pictured in Fig. 2(d). In a typical experiment (Barth, 1938) the rate of regeneration of the proximal hydranth was 21.3 when the distal end was so treated, as compared with 4.0 and 2.7 when the former was in competition with an actively regenerating distal region.

TABLE 1

Comparison of rates of regeneration of proximal ends with and without competition with the distal end (Barth, 1938)

EXPERIMENT	NO. OF STEMS	LENGTH IN MM.	RATE IN COMPETITION	RATE IN ISOLATION
A	6	5.0	0	36.8
B	14	7.5	0	31.9
C	14	7.5	3.9	15.1
D	10	10.0	10.7	35.9
E	10	10.0	4.4	13.0
F	10	10.0	0	8.6
G	10	13.0	41.7	53.0
H	10	13.0	17.9	28.1
I	10	15.0	12.6	26.8
J	10	15.0	18.8	20.4
K	10	20.0	19.0	28.9
L	10	25.0	29.0	47.4
M	10	25.0	27.9	34.0

It is of interest to see whether our particular interpretation of the coefficients of interaction is supported by the experimental data. Their existence as far as kinetic equations are concerned has the overall effect of decreasing the rates of transformation. Since they are presumed to vary inversely with the total physiologically connected volume, any increase in the latter, by decreasing the numerical magnitudes of these coefficients, should result in a general increase in rate. Such experiments can be performed by comparing the

rates of differentiation of the proximal ends of stems under the conditions pictured in (b) and (c) of Fig. 2. In two typical experiments of this type, in which a total of 2.7 x $10^7\mu^3$ were added to the proximal end by moving the ligature distally a 50 per cent increase in regeneration rate was obtained, and in another the addition of 1.8 x $10^7\mu^3$ resulted in a 107 per cent increase.

These results have a certain critical value for the evaluation of the importance of physiological competition in the regulative mechanism of developmental processes. The fact that the competition hypothesis can predict rate variations in the transformation of an isolated group as a consequence of changing the amount of physiologically connected volume would appear to argue in favor of its playing a role in normal regulation. Indeed, it was experiments of this nature that first led to the invocation of competition phenomena as necessary for a more complete description of the facts (Barth, 1938, 1940).

EXPERIMENTS ON THE TIME COURSE OF DOMINANCE RELATIONS

In discussing the kinetic characteristics of physiological dominance, certain deductions were made directly from the assumption that the underlying mechanism was physiological competition. We shall in what follows see how closely they fit some available experimental facts. For the sake of simplicity in the comparison, they are listed in the following fashion:

1. A fully formed structure can regulate the extent of transformation of any lower potential region with which it is connected.
2. The intensity of the physiological dominance exerted by a group increases as it approaches the end of its transformation and attains a maximum value when the process is completed.
3. As corollaries to 2, the theory demands a dependence of dominance intensity on the interval between the stimulations to activity such that
   (a) If the group with the greater potential is started first, the longer the interval to the onset of the transformation of the lower potential group, the greater will be the intensity of the inhibition of the latter.
   (b) If no dominance exists between two groups, such can be made to appear by delaying the stimulation to differentiation of one or the other. By this means normal dominance relations may be reversed, and proximal groups made dominant to distal ones.

In an interesting series of experiments Watanabe (1935) presents data which offer the opportunity of subjecting the above conclusions to experimental tests. An ingenious experimental device allowed him to measure dominance intensity with relative ease. He employed pieces 15 to 20 millimeters in length from the distal stem regions of *Corymorpha* individuals. Such sections will almost invariably develop hydranths at both ends under normal conditions. By varying the conditions of the preparations of the stem sections, he could cause

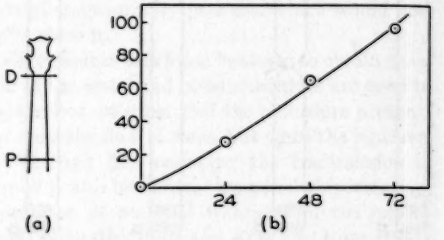

FIG. 3. REGULATIVE ACTIVITY OF AN ADULT HYDRANTH
(a) Experimental procedure. Proximal section at P at 0 hours; distal section at D at (0, 24, 48, 72) hours.
(b) Graph of results. Ordinates, percentage of unipolar forms; abscissae, hours; 50 pieces in each lot. (After Watanabe, 1935.)

the suppression of either distal or proximal hydranths in these normally bipolar forms. Evidently the different preparation methods varied the dominance intensity of the two ends with respect to each other, and it was possible to measure the resulting changes in dominance by the frequency and kind of unipolar forms in the treated stems. The method had the added advantage that it measured the phenomenon in the whole range from zero to 100 per cent dominance.

The basic idea behind the procedure was the employment of the delayed cut. Thus, in one series of experiments, a proximal section was made first at P (Fig. 3a), leaving the hydranth on the stem for varying lengths of time before it was removed by sectioning at D. This procedure, then, tests the ability of the fully formed hydranth to regulate proximal reconstruction. As is shown by the graph of the results (Fig. 3b), the frequency of proximal hydranth suppression rose uniformly

from zero with no delay to almost 100 per cent when the delay of the proximal cut was about 72 hours. Aside from the direct verification of conclusion 1, the smooth rise of the dominance with the length of the delay is itself an interesting confirmation, for it would be expected that the longer the proximal portion is under the maximal influence of the complete structure, the severer the resulting inhibition would be.

Conclusion 2 and its corollary 3a are interestingly confirmed by the following experiment. Using the same kind and length of stems, a section was first made distally at *D* (Fig. 4a), and the proximal ones at *P* were made at various intervals after the initial cut. The data obtained are illustrated by Fig. 4b. It is immediately evident from

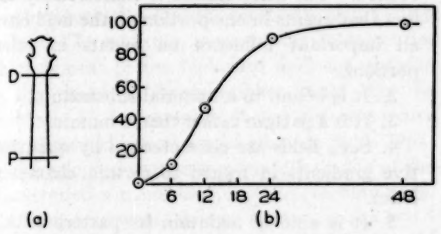

FIG. 4. INCREASING DISTAL DOMINANCE

(a) Experimental procedure. Distal section at D at 0 hours—proximal section at P at (0, 6, 12, 18, 24, 48) hours.

(b) Graph of results. Ordinates, percentages of unipolar frequency; abscissae, hours; fifty pieces in each lot. (After Watanabe, 1935.)

the curve that the desired dependence of dominance intensity on the length of the interval of delay obtains during the course of development. The intensity rises quite steadily during the development of the dominant group, to attain a maximum value with the formation of a complete hydranth.

We may now turn our attention to some data which afford a test of corollary 3b, concerning dominance reversal. In particular, it is desired to test the implication that a suitable adjustment of the time relations could make a proximal group dominant to a distal one.

Using stems of exactly the same nature as employed in the previous experiments, simultaneous sections were made at *P* and D_1 (Fig. 5a). At various later times another distal section was made at D_2. The resulting new distal region, therefore, starts its transformation under the competitive influence of the proximal group at various stages of development. Figure 5b gives the data from an experiment of this type. It is clear from the curve that conclusion 3b is confirmed. As would be expected from the similarity of the kinetic equations for the two groups, this kind of reversed dominance follows the same upward trend with increasing delay of starting the distal group on the way to differentiation. However, it is interesting to note that the same 48 hour period of delay produced only a 63 per cent proximal dominance, whereas in the reverse case an almost 100 per cent distal dominance was obtained.

It would be desirable to repeat these experiments using the tube method (Fig. 2d) of inhibiting transformation activity. This would avoid

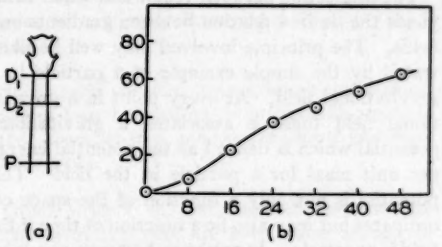

FIG. 5. DEVELOPMENT OF PROXIMAL DOMINANCE IN CORYMORPHA

(a) Experimental procedure. Section at P and D_1 at 0 hours; second distal section at D_2 at (0, 8, 16, 24, 32, 40, 48) hours.

(b) Graph of results. Ordinates, percentage of unipolar forms at proximal ends; abscissae, hours. Fifty pieces in each lot. (After Watanabe, 1935.)

disturbing the physiological volume relationships and would also have the advantage of keeping the same levels under study throughout the experiment.

THE RELATION BETWEEN THE COMPETITION HYPOTHESIS AND THE FIELD CONCEPT

The development of competition as a regulative factor has depended rather heavily on gradients. Consequently, some answer to the problem of whether physiological competition can be incorporated into a field theory may be sought in the connection between gradients and fields. It is desirable to begin with a brief examination of the field concept as it has developed in physics, in which science the general abstract notion of a field has received its most complete development.

The physical concept of a field stems from the assumptions of the continuity of space and the indestructibility of energy. Further development

along this line served to focus attention on the possibility of examining phenomena from the viewpoint of a physical continuum with the aid of field equations. There are in general two types of fields, vector and scalar. A vector field is one in which every point is associated not only with a magnitude but also with a direction. An example of a vector field is a field of force that may be defined as a continuous region of space at every point of which there is defined the force (in magnitude and direction) that would act on a standard particle placed there. Scalar fields are characterized by a numerical value at every point independent of direction. A potential field is a scalar field.

The connection between vector and scalar fields yields the desired relation between gradients and fields. The principle involved may well be illustrated by the simple example of a particle in a gravitational field. At every point in a gravitational field there is associated a gravitational potential which is defined as the potential energy per unit mass for a particle in the field. This potential is not only a function of the space coordinates but may also be a function of time if the field is nonstatic. In any case, however, the value at any given point in the region is not dependent on any particular direction and hence it is a scalar field. The most important characteristic possessed by a potential field is that the negative of its gradient is the force per unit mass, often designated as the strength or intensity of the field. Mathematically, if V denotes the potential and $\vec{F}$ the force or intensity, the latter is given by

$$\vec{F} = -\left(\vec{i}\,\frac{\partial v}{\partial x} + \vec{j}\,\frac{\partial v}{\partial y} + \vec{k}\,\frac{\partial v}{\partial z}\right)$$

with x, y, z being the coordinates and $\vec{i}$, $\vec{j}$, and $\vec{k}$ the unit vectors along the x, y and z axes respectively. It is clear from this equation that the simultaneous absence of potential gradients along the three coordinate axes implies the absence of force. Furthermore, it is physically meaningless to separate the force field from the gradients of potential.

A. The Biological Field

Essentially, what has been accomplished by the field concept in physics is the possibility for a unique description of the motion of matter in terms of the properties of space. The resultant field equations possess a characteristic unity, since only a single such equation is necessary for the description of the entire region. It is this unitary characteristic of the field theory which has impressed biologists with its possible utility for describing morphogenetic events. In adopting the term 'field' for biological usage, it was sought to emphasize the interconnection of morphogenetic events and the interdependence of the parts of the developing organism. Subsequent elaboration of these primary ideas has led to the field theory of development.

A brief description of a biological field may be presented in terms of the characteristics which it has been presumed to possess (Weiss, 1939; Huxley and de Beer, 1934).

1. A field is a spacial unity which is interrelated. The interrelation is expressed by the fact that events in one portion of the field have an important influence on events in other portions.
2. It is bound to a material substratum.
3. It is a pattern rather than a mosaic.
4. Such fields are characterized by quantitative gradients in regard to certain characteristics.
5. It is able to maintain its pattern within certain limitations when its mass is reduced and can perpetuate its pattern when completely divided into two or more pieces.
6. It is able to maintain its pattern when its mass is increased, and to fuse with similar patterns entering with the new material if the axial orientations are favorable.

It may be mentioned in passing that these six characteristics are not all logically distinct. This is true, for example, of 3 and 4. The assumption of gradients presupposes a continuity which would prohibit a mosaic pattern. The latter implies the existence of discontinuities and singularities which are not permissible within a field generally, though they may occur at its boundaries. In point of fact, a separate postulation of gradients is not logically necessary since the assumption of a field implies their existence (see below).

It will be noted that in the development of the biological concept of the field, insofar as the problem is considered, the main emphasis has been on the matter rather than the space. Thus we have a field whose "matter" can be increased and decreased. Little criticism can be leveled at the emphasis since, after all, the very data to be considered focus our attention on the morphology of the material rather than the space around it.

The failure of a close parallel evolution of the two has many reasons in addition to that already mentioned. One of the most important, which has seldom been clearly recognized, is the existence of a dichotomy in the problem of morphogenesis which prevents at once the direct application of the simple field concept. Morphogenesis consists not only of the movement of matter through space, which yields the changing form of the developing organism, but also involves the transformation of matter from one type into another, a process which has been named by some "chemical differentiation.'

Some conciseness in thinking could be gained if this were clearly recognized. The problem could then be reduced to some of its more elementary components, each of which may be simpler of solution that the composite picture they present. In addition, some of the incongruities which appear in the biological field concept due to the union of incompatibles would thus be avoided. If, for example, it was agreed to consider force fields and transformation fields separately, a logical segregation could be made of the characteristics mentioned on the preceding page. The force field would possess characteristics 1 to 4 inclusive, whereas the transformation field would be described by all six.

Some objections may be raised against this procedure, but it has its precedents in physics, in which science a single unified field theory is yet to be attained. The greater precision of definition possible would allow a closer and more exact examination of those fields which are more uniquely biological, i.e., the transformation fields.

Another advantage which may accrue from this procedure of separation is the development of a method of transfer from the physical to the component biological field. The inability to do so with the field concept as described by the six characteristics stems, as we have seen, from the attempt to lump all phenomena into a single biological field theory. This barrier is to a certain extent removed by the proposed segregation. The elimination of some of the physical inconsistencies permits the transfer of certain useful basic concepts. One such fundamental relation which may be mentioned is that between field and gradient in their most general sense, and about which some confusion has existed.

There has appeared at various times in the literature a curious schism between the so-called gradient hypothesis and the field concept. Certain authors, while not hesitating in their acceptance of the field concept, go to great lengths in their arguments against the existence of gradients. Other authors who accept both, do so on the "individual merits" of each. In still other cases the two ideas are combined in a fashion which would imply a separation that is not inherent in the field concept as it has thus far been understood and developed. Thus Huxley and de Beer (1934) state:

> "*Within these morphogenetic fields* various processes concerned with morphogenesis appear to be quantitatively graded so that the most suitable name for them is gradient systems or simply gradient fields." (Italics added).

Again, in a slightly later paper Huxley (1935) writes;

> "Such fields are always characterized *during certain* stages at least by quantitative gradients in regard to certain characteristics, and these gradients may be of various forms.

Other writers, in discussing the relative importance of the two, are even more definite in their implications that fields can exist distinct from gradients. Our discussion of the simpler physical field would deny this possibility since it showed a close and inseparable relation between the two. A field in which gradients are completely absent can effect neither the motion nor the transformation of matter and cannot therefore be invoked as a causal or descriptive agent for either. In the same vein it is meaningless to bring up the question (Needham, 1942) as to which is more fundamental, the gradient or the field? One may as well ask, which is more fundamental in determining velocity, distance or time?

One must admit that the relation between gradients and fields is not immutable. The two terms are, after all, words whose connotations may be altered at will. However, in those cases where such is the intent, a more explicit definition would be helpful.

B. Fields of Physiological Competition

To avoid unnecessary complications in the following discussion an inverse relation between the potential and interaction coefficients of a group will be assumed, as in Case 3. This permits an analysis which requires a knowledge of the potentials only, for determining the properties

and subsequent behaviour of the system. In the preliminary development of competitive morphogenetic fields, the following questions will be kept in mind.

1. How many and which of the listed characteristics of a biological field do they possess?
2. Can they be more precisely defined than has heretofore been possible in the case of biological fields?
3. Does the theory provide a mechanism for interaction within the field?
4. In terms of the postulated interaction mechanism, can it provide a reasonable explanation why a field normally "realizes but a single actuality?" (This important question was raised by Huxley, 1935, in a discussion of the properties of biological fields.)

It is necessary at the outset to agree upon a unit, analogous to the test particle of physics, in terms of which we can both define a field and assess its qualitative and quantitative characteristics. The nature of this unit must ultimately be referable to the available experimental techniques if the theory is to have experimental consequences. Let us call this unit a 'group' and agree to mean by this term the smallest amount of material which can be experimentally handled. In some cases, as in blastomere experiments, the units will be simple cells. In others, as in many transplantation experiments in amphibian material, it will signify a group of cells. For present purposes, the only further qualification that is necessary is that no significant potential difference exist between any two elements of a group. Under such circumstances the conclusions are in general independent of group size.

Each group will be characterized by a set of parameters, among which we may mention differentiation potentials, coefficients of interaction, and coefficients of environmental resistance. In terms of these units, and the basic concept of physiological connectivity developed earlier, we may then set up the following definition of a field:

A field of physiological competition is a collection of physiologically connected groups.

Further development proceeds along the lines of a simple generalization of the considerations already met with the interaction of two groups. From the previous discussion it is known that a set of two equations is necessary for an adequate description of the interaction effects between two groups. Consequently a field such as has just been defined will not be described by a single field equation as in physics, but by a system of equations the number of members of which will correspond to the number of groups in the field. Thus, for n such groups, we would have:

$$\frac{dR_1}{dt} = (K_1 - R_1)\left(b_1 - \lambda_{11} R_1 - \sum_{i=1}^{n} \lambda_{1i} R_i\right)$$

$$\frac{dR_i}{dt} = (K_i - R_i)\left(b_i - \lambda_{ii} R_i - \sum_{\substack{j=1 \\ j \neq i}}^{n} \lambda_{ij} R_j\right)$$

$$\frac{dR_n}{dt} = (K_n - R_n)\left(b_n - \lambda_{nn} R_n - \sum_{i=1}^{n-1} \lambda_{ni} R_i\right)$$

In terms of these equations there exists the following precise, necessary, and sufficient condition that two groups by members of the same field:

Two groups are members of the same field when, and only when, the dependent variable R_i of one appears in the differential equation describing the transformation kinetics of the other.

By the same token, we have for physiological isolation either one of two conditions:

(a) A group is physiologically isolated if its coefficients of group interaction with respect to all other groups are zero; or

(b) All the R's of all connected groups are zero.

While, as we have seen, the kinetic effects would be the same, the biological and experimental methods of arriving at the isolations defined by these two conditions are quite different. To distinguish them, condition (a) might be called "absolute isolation," implying a real physiological disconnection, whereas condition (b) might be named "effective isolation."

Not all fields defined by the above system of equations are functional in regulating the transformations of its member groups. It will be remembered that even with positive, finite values for both the λ_{ii}'s and the R_i's a gradient in potential is still necessary for regulatory activity. Analogous to the uni-dimensional case discussed previously we may then state in terms of the components of the gradients along the three coordinate axes x, y, and z, that a necessary

condition for the existence of a functional field is that

$$\left(\vec{i}\,\frac{\partial b}{\partial x} + \vec{j}\,\frac{\partial b}{\partial y} + \vec{k}\,\frac{\partial b}{\partial z}\right) \gtrless 0$$

Non-functional or non-regulatory fields, given by changing the above to an equality, are of no interest in the description of organized morphogenesis.

In addition to the existence of potential gradients, there are certain other relations, derivable from the known properties of competitive interaction, which must obtain within a functional field. Let us define an iso-potential line as one along which the gradient in potential is zero. Similarly equi-potential groups are ones that have equal b values. The following characteristics of a competition field are then immediately deducible:

(a) No unilateral regulatory activity can occur between equi-potential groups.

(b) Dominance will not occur along iso-potential lines.

(c) Any field which has a potential distribution such that only one group possesses the maximum potential, will "realize but a single actuality" if all lower potential groups have values equal to (or very little greater than) the minimum amount of differentiation required for the realization.

(d) Within a single field multiple realizations will occur if more than one group possesses the maximum potential. Such maximal-potential groups, since they are equipotential with respect to each other, will complete the process without differential inhibitory interaction.

(3) Multiple realizations may occur in a field with a single maximum if some of the lower potential ones possess $\frac{\lambda_{ii}}{b_i}$ sufficiently above the critical minimum R_i value so that the regulation of the maximal group does not depress the steady state $\bar{R}_i$ of these groups below that minimum.

A pictorial representation of some of these characteristics may be obtained by plotting potential against distance from some arbitrarily selected axis. If it is desired to secure a two dimensional representation such that all the points in each distance-potential plane will belong to the same competition field, then r potential profile through the maximum may be made. Thus, with ordinates representing potential and the abscissae distance from the reference axis, Fig. 6a illustrates an unimaximal field and Fig. 6b one with two equipotential maxima at A and B so that both points realize their potentialities. The eye field in general, and in particular of the chick, investigated by Willier and Rawls (1935) is an example of one containing two equipotential maxima.

Without further analysis it is apparent from the above description that fields of physiological competition possess the important feature of the inter-relation of units. We may now briefly inquire whether they are also characterized by an independence from initial conditions implied by properties 5 and 6 listed in page 140. It must of course be realized that qualifying limits of reasonableness are imposed on this independence, for a certain minimal amount of tissue must be initially present to form a complete structure.

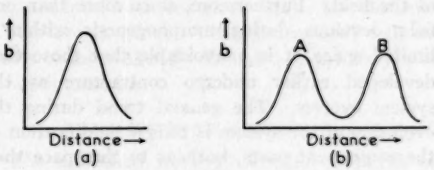

FIG. 6. DIFFERENTIATION POTENTIAL PROFILES THROUGH MAXIMA
(a) Field with a single realization.
(b) Field with multiple realization of equi-potential groups.

The problem can most easily be examined by writing down the steady state value of R for a group i competing with a group j. Analogous with equation (25), this takes the form

$$\bar{R}_i = \frac{\lambda_{jj} b_i - \lambda_{ij} b_j}{\lambda_{jj}\lambda_{ii} - \lambda_{ij}\lambda_{ji}}$$

This expression contains none of the integration constants which are determined by the initial conditions. (Note that this is also true for the isolated group where the steady state value for effective competitive interaction is given by $\frac{b_i}{\lambda_{ii}}$. Thus unless the initial conditions are severe enough to express themselves indirectly through the interaction coefficients, the steady state values are independent of them. This more or less relative independence from initial conditions is a special case of a widespread phenomenon characteristic of all systems entering the steady state. Consequently, this property will be pos-

sessed by all transformation fields which require energy for maintenance. A more detailed examination of this interesting phase of the problem is beyond the scope of the present paper.

In addition to the above mentioned properties there exist certain general implications of the competition theory, as well as its field theory generalization, which are of importance to various other aspects of the general problem of embryogenesis.

Morphogenetic Plasticity

Since the theory predicts increasing regulative intensity in the course of the development of the dominant group, it is inevitable that the other members of the field lose their potentiality for transformations as long as they remain members of the field. Furthermore, since more than one field develops during morphogenesis within a limited space, it is unavoidable that those that developed earlier undergo contracture as the system evolves. The general trend during the evolution of the system is thus a rigidification of the component parts, both as to the space they can occupy, as well as to the transformation levels they can achieve as members of an organismic whole.

The same theoretical implications lead to an interesting interpretation of the onset of transformation in an established system. According to the theory developed, one of the critical factors which maintains the rigidity of the adult pattern is the existence of the dominant group which acts as a regulator in its adult form. Consequently, to induce differentiation in some other region of the field, it is sufficient to remove the maximal potential group. From this point of view then, the onset of the formation of, for example, a new hydranth in a coelenterate when the old structure is removed is mainly due to the removal of an inhibitory regulative activity. It is not necessary to postulate any specific stimulations due to cutting or other concomitant changes, though such cannot of course be ruled out. Such interpretations of the nature of regeneration in adult organisms are not new, having been admirably elaborated by Child (1941) and more recently by Rose and Rose (1941) in their experimental analysis of hydranth reconstitution in *Tubularia*.

Maintenance versus Morphogenetic Energy

Inherent in the basic concepts of the competition hypothesis, as well as in the above interpretation of the nature of the stimulation to regeneration, is the implication that the fundamental energy-yielding mechanism for the maintenance of an adult structure is intimately related to, if indeed it is not one and the same as, that utilized in its embryonic formation. A relation of this kind is difficult to deny in the face of the demonstrated ability of adult structures to control the constancy of organismic pattern. A plausible explanation may be made in terms of the utilization of a critical substrate. Experimentally, this would imply that a utilizable method of approach to the problem of, for example, the energetics of hydranth regeneration is the study of the adult hydranth itself and particularly those energy-yielding processes necessary to maintain its structural integrity.

The same viewpoint would also question the validity of recent attempts (see Needham, 1942, and Tyler, 1942, for discussions) to separate so-called 'maintenance' metabolism or energy from its morphogenetic counterpart. Thus, within the theory of competitive interaction it would be impossible to set up a definition of differentiation as "simply those processes not included under what we regard as maintenance."

We may cite an analogous situation in the growth of a population to make the point at issue clearer. When bacteria are seeded into a broth culture, it is well known that after an initial lag period, they enter into the exponential phase of their growth curve, which gradually tapers off as the population enters the stationary phase. It would be clearly meaningless here to set up a qualitative distinction of the energetics involved in the exponential period as compared with that involved in maintaining the population at the stationary level. The mechanism for keeping the population density constant is the production of new individuals to replace those that have perished. Thus the only difference between the exponential period and the stationary state of the growth curve is that in the former the rate of production of new individuals exceeds the death rate of already existent ones, whereas in the latter the two rates are equal. The fundamental energetics for the production of a new individual is the same no matter what part of the history of the population is being studied.

Precisely the same fundamental kinetic mechanisms are involved in the formation of a new cell or in the transformation of one type into another. It is undoubtedly true that "structural death" is continually occurring in a cell, necessitating a replacement mechanism. For the production of a new cell it is only necessary that the rates of syntheses of new structure exceed the normal rate of destruction. For its maintenance it is sufficient that they be equal. With each synthesis of a new structural unit there must occur a parallel qualitative and quantitative change in the "maintenance" energy required to keep the system at the new transformation level. Thus the energetics of maintenance and new syntheses become indistinguishable in nature except for a quantitative characteristic involving the difference between two rates.

There are other characteristics of these transformation fields which it is desirable to analyze. For example: precisely what does it mean to say that a given group of cells does not reach a particular transformation level but a lower one? Are all transformation levels realizable? In other words, does every point on the path of differentiation to a complete structure represent a point of sufficient stability such that the group will remain there if stopped? An examination of the problem from an energetics point of view would suggest an answer in the negative. A more likely situation would imply the existence of quasi-stable points, such that if a group found itself halted between two of them, it would go to one or the other, depending on the conditions of the energy flux rate. According to this concept, several quite different morphological and histological pictures could very well represent different levels along the same transformation path. And whether a particular group ends up in one rather than another would depend on its differentiation potential with respect to other members of the field.

In this connection mention may be made of Yamada's (1940) extremely interesting researches on the fate of chorda-mesodermal isolates of the salamander neurula. He found that presumptive blood islands, when isolated, yielded only blood island cells, but when a bit of notochord was included with the isolate, there resulted in addition to blood island cells, pronephros and some muscle. On the other hand, presumptive pronephros yields mainly pronephros and blood island cells. When, however, notochord is included in the isolate, muscle makes its appearance in 38 per cent of the cases. He was thus able to "raise" tissue "above" its prospective significance. He arranged the tissues in order of "morphogenetic potential" and interpreted his data in those terms.

However, such problems cannot be analyzed within the confines of the limitations imposed on the present analysis. An entirely different level of organization involving the energetics and points of stability of flux equilibria must be the basis for their adequate examination.

In summary, it may here be said that both the special and general properties found for the competitive transformation fields coincide in many ways with those of the biological field concept. The formulation provides reasonably precise definitions of fields and field membership, as well as an interaction mechanism in terms of which experimental consequences may be deduced. These are in general three-dimensional counterparts of those already discussed in the section on group interaction.

ACKNOWLEDGEMENT

The published work of Dr. L. G. Barth on hydroid regeneration served as the stimulus for the present analysis. My indebtedness to Dr. Barth is, however, even more direct. When the idea of elaborating a developmental theory along these lines was first proposed to him by the author, his immediate enthusiastic encouragement was the impetus that initiated it.

I should also like to take this opportunity to express my gratitude to Dr. H. B. Steinbach and Dr. V. Hamburger for their patient guidance during the various developmental stages of the manuscript and for very many helpful and suggestive conversations.

SUMMARY

An attempt has been made to develop a theory which would provide a regulatory mechanism for morphogenesis in terms of which potency limitation could be described.

Child's concept of physiological dominance has been examined, with especial attention focused on its logical relation to the gradient theory. It has been shown that an activity gradient *per se* has but limited explanatory usefulness unless it is implemented with an effector mechanism. Only then can dominance and other regulatory characteristics emerge.

A mechanism based on the competitive interaction of the transforming cells has been developed, several cases of graded biological complexity being examined. In terms of the theory, potency limitation was predicted, and its characteristics were examined. Precise conditions involving activity gradients have been deduced for the presence or absence of regulatory phenomena.

In terms of such parameters as differentiation potentials and coefficients of internal and group interaction, certain testable conclusions were deduced concerning transformation end-points and kinetics. In particular, the theory demands a dependence of dominance relations on the transformation levels arrived at by the various groups during the evolution of the system.

The above deductions and relations have been compared with available data on hydranth reconstitution in coelenterates.

The relation between the competition theory and the field concept has been analyzed. The examination permitted a rational generalization to a field theory of competitive interaction. The properties of such transformation fields have been compared with both physical and biological fields as they have been developed. The formulation permitted a reasonably precise definition of fields and field memberships.

LIST OF LITERATURE

ADELMANN, A. B. 1929a. Experimental studies on the development of the eye, I. *J. Exp. Zool.*: 54, 249–290.

——. 1929b. Experimental studies on the development of the eye, II. *J. Exp. Zool.*: 54, 291–317.

BARTH, L. G. 1938. Quantitative studies of the factors governing the rate of regeneration in *Tubularia*. *Biol. Bull.*, 74: 155–177.

——. 1940. Regeneration in hydroids. *Biol. Rev.*, 15: 405–420.

BOVERI, TH. 1901. Über die Polarität des Seeigeleies. *Vhl. phys. Med. Geo. Würzburg*, 34: 145–175.

CHILD, C. M. 1907. An analysis of form regulation, I, II, III. *Arch. EntwMech. Org.*, 23: 396, 415, 445.

——. 1929. Lateral grafts and incisions as organizers in the hydroid, *Corymorpha*. *Physiol. Zool.*, 2: 342–374.

——. 1932. Determination of new axes by lateral graft and incisions in *Corymorpha* in relation to the gradient and dominance. *Physiol. Zool.*, 5: 593–627.

——. 1941. *Patterns and Problems of Development*. Chicago: University of Chicago Press.

CLARKE, L. F. 1936. Regional differences in eye-forming capacity of the early chick blastoderm as studied in chorio-allantoic grafts. *Physiol. Zool.*, 9: 102–128.

DRIESCH, H. 1897. Studien über das Regulationsvermogen der Organism, I. *Arch. EntwMech. Org.*, 5: 389–.

GURWITSCH, A. 1922. Über den Begriff des embryonalen Feldes, Arch. *EntwMech. Org.* 51: 383–415.

HUXLEY, J. S. AND DE BEER, G. R. 1934. *The Elements of Experimental Embryology*. Cambridge, Eng.: Cambridge University Press.

HUXLEY, J. S. 1935. The field concept in biology. *Trans. Dynamics Devel.*, (USSR), 10: 269–.

MORGAN, T. H. 1903. Some factors in the regeneration of *Tubularia*. *Arch. EntwMech. Org.*, 16: 125–.

NEEDHAM, J. 1942. *Biochemistry and Morphogenesis*. Cambridge, Eng.: Cambridge University Press.

REINER, J. M., AND SPIEGELMAN, S. 1944. The energetics of transient and steady states. *J. Phys. Chem.* (in press).

ROSE, M. S., AND ROSE, F. C. 1941. The cut surface in *Tubularia* regeneration. *Physiol. Zool.*, 14: 328–.

SCHOENHEIMER, R. 1940a. *The Dynamic State of Body Constituents*. Cambridge, Mass.: Harvard University Press.

——. 1940b. The synthesis of protoplasm constituents. Second Symposium on Growth and Development. Growth (Supplement).

SPIEGELMAN, S., AND F. MOOG. 1944. On the interpretation of rates of regeneration and the significance of the independence of mass and time. *Biol. Bull.*, 87: 227–241.

SPEMANN, H. 1938. *Embryonic Development and Induction*. New Haven: Yale University Press.

THOMPSON, D'ARCY. 1942. *Growth and Form*. 2nd ed. Cambridge, Eng.: Cambridge University Press.

TYLER, A. 1942. Developmental processes and energetics. *Quart. Rev. Biol.*, 17: 197–212; 339–353.

WATANABE, Y. 1935. Physiological dominance in *Corymorpha palma* in relation to reconstitution and methylene blue reduction. *Physiol. Zool.*, 8: 417–441.

WEISS, P. 1939. *Principles of Development*. New York: Henry Holt and Co.

WILLIER, B. H., AND RAWLS, MARY. 1935. Organ forming areas in the early chick blastoderm. *Proc. Soc. Exp. Biol. Med.*, 32: 1293–1296.

YAMADA, T. 1940. Beinflüssung der Differenzierungsleistung des isolierten Mesoderms von Molchkeim durch Zugerfügtes Chorda and Neuralmaterial, *Fol. Anat. Jap.*, V. 19: 131–198.

ZWILLING, E. 1939. The effect of removal of perisarc on regeneration in *Tubularia corcea*, *Biol. Bull.*, 76: 90–103.

MIMETIC POLYMORPHISM, A CONTROVERSIAL CHAPTER OF DARWINISM

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Preface

ABOUT fifteen years ago a small dinner party made up of J. S. Huxley, J. B. S. Haldane, A. R. Fisher, E. B. Ford, and the present writer met at the Athenaeum Club in London. I do not remember the topic of the conversation, but Haldane was preparing a book on the causes of evolution, Fisher had his well known book in press, Ford was to make a special study of mimetic polymorphism, and Huxley was to edit the *New Systematics* and to write a book on evolution in which mimetic polymorphism was to be treated in the light of the views of Fisher and Ford. If the conversation and discussion had turned to the topic of mimicry I should probably have stated my views similarly to the contents of the following paper. Had this been the case, it would certainly have been a lively, if not heated discussion, but nevertheless one among friends. In such a spirit the following critical discussion is presented.

INTRODUCTION

Ever since evolution became the central problem of zoology, students in this field have turned their attention to the wing pattern of Lepidoptera. Already Bates, Wallace, and Darwin had discussed the cases of apparent mimicry from the standpoint of selection; Müller continued the study of mimicry in Lepidoptera and found important principles, now bearing his name. Eimer used predominantly the pattern of butterflies as a basis for deriving his theory of orthogenesis. Weismann first started the study of experimental evolution in his work on temperature action upon the wing pattern of butterflies. He was followed by a whole school of experimenters, led by Standfuss, Fischer, Merrifield and Countess Linden (complete bibliography in Biedermann, 1912) who tried to solve phylogenetic problems in Lepidoptera by temperature experiments involving the wing pattern. All of these authors and their followers had the feeling, if not the conviction, that a considerable part of the secret of evolution lay hidden behind the manifold and beautiful patterns of Lepidoptera, and that an understanding of these patterns would constitute a large step towards the explanation of evolution. The present author, followed by Kühn, carried this conviction into the present era.

Among the many specific problems attacked was one which came to the foreground in many subsequent discussions: that of mimicry in butterflies, both in the form of mimicking the environment (e.g., leaves) and of mimicking other protected animals (e.g., wasps). In the latter group belong, as a specially interesting set of facts, those remarkable cases in which butterflies of one group mimic others belonging to another family whose members are supposed to be protected by poisonous juices or repellent taste. The interest in these phenomena, which had already been thoroughly discussed by Wallace and Darwin, was reawakened when the rising tide of Mendelism led to a new evaluation of selection. It was De Meijere (1910) who first furnished genetic information upon the subject; while Punnett (1915), whose student Fryer had succeeded in analyzing another case, took up a discussion of the whole problem from the viewpoint of genetics. Punnett's general conclusion was that selection of small mutants could not explain the origin of the genetic system involved in these cases. In a discussion of some problems of evolution from the standpoint of physiological genetics (Goldschmidt, 1920), I accepted Punnett's explanation and tried to point out some facts regarding pattern formation which I considered to be in favor of Punnett's viewpoint. Some years later a completely new point of view was introduced by R. A. Fisher (1927–30), derived from his general theory of the origin of dominance by selection of modifiers in the heterozygote. A

parallel idea was developed for the origin of the mimetic patterns. These ideas were taken up most enthusiastically by Fisher's former student, E. B. Ford (1936–40), who made special studies of the actual material in order to prove Fisher's point.

In all these discussions (with the exception of that in my book, 1920a) one decisive group of facts was completely left out of account, namely, that pertaining to the determination of wing pattern in butterflies. I returned to the subject (Goldschmidt, 1927) and tried to formulate a model of pattern formation in the complicated cases of mimicry, based upon Punnett's genetical interpretation and upon a generalized theory of genetical control of all patterns. In a recent paper, Ford (1936, p. 444) remarked that one element in my explanation, the track for the spread of melanin, does not conform to that actually observed in intermediates. Though my explanation was meant only as a model, not as a literal explanation, for which the data had been missing, Ford's criticism is justified in so far as I failed to take into account sufficiently the knowledge of pattern formation which was beginning to accumulate at the time of my writing. Actually a considerable body of factual information has been found since: descriptive and experimental embryological knowledge of the pattern and its determination (Goldschmidt and students, and especially Kühn and students); the comparative morphology of pattern (Schwanwitsch, Süffert, Kühn, Henke); experimental shift of pattern (Goldschmidt and students, Kühn and students); phenocopies in regard to pattern (Standfuss, Fischer, Goldschmidt, Kühn); the genetics of pattern elements (numerous authors, especially Cockayne, Federley, Ford, Gerould, Goldschmidt, Harrison, Onslow, *et al.*). Under these circumstances a renewed analysis of the entire problem seems of interest, especially as many evolutionists are not aware of most of the work, just mentioned, many geneticists are cognizant only of work done with their special pet animal or plant, and many embryologists are neither interested in insects or in genetical analysis. I feel encouraged to try such an analysis not only because I have myself performed experiments and done morphological work on many of the groups of facts involved, but also because I have considerable first-hand information on the other aspects, since, for example, Süffert's work on seasonal dimorphism and his comparative work on pattern was done in my laboratory, as was also Henke's elaborate work on pattern in Saturnid moths. I had, further, a chance to go carefully over the specimens from Fischer's famous temperature experiments and of Standfuss' breeding experiments (through the courtesy of Consul Biedermann in Zurich); I was able to observe in nature (in Java) some of the famous cases of mimicry and had the privilege of being shown by the late Professor Poulton his many boxes of families of *Papilio dardanus* upon which, later, much of Ford's work was based. Thus, what errors I may commit in the evaluation of the data are not based upon lack of first-hand information.

THE BASIC FACTS OF MIMICRY (MIMETISM)

A. Ecology

We shall not discuss here the ecological basis of our problem, i.e., the proofs that the mimetic forms actually mimic their model. If this were not the case, the entire problem would be only one of variation, without major importance for the understanding of evolution. The scholars who are mainly responsible for the elaboration of the principle of mimicry, Bates, Wallace, Darwin, Müller, and more recently, Poulton, and Carpenter have established the criteria for mimicry: relative scarcity of mimic as compared with numbers of model, rejection of the model by many predators, presence in the same locality and simultaneous flight. The data, collected by the best field observers, have been scrutinized many times. Not all points are perfectly clear, and there is a certain mass of non-conforming facts. But, as a whole, the mimicry theory stands the tests made, and the majority of trained observers, as well as theoretical evolutionists, accept the evidence. (For the most recent review see Cott, 1940, and Carpenter's discussion with Shull, quoted below.) There has been opposition to the interpretation as mimicry of the cases under discussion, as well as against the theory of mimicry as a whole (e.g., Heikertinger, Shull, Attee). But there are not many observers with field experience who belong to this group. Thus we accept the mimetic resemblance of the groups of butterflies under discussion as an established fact, but without denying that sometimes mimicry is claimed in rather dubious cases.

B. Simple and sex-controlled polymorphism

The typical cases of mimetism (as sometimes the special type of mimicry under discussion is called) are found in the following groupings:

1. Both sexes of a species of a butterfly are dimorphic. The best example (best, because genetic information is available) is *Hypolimnas dubius* Beau. from Africa, (Family Nymphalinae). On the west coast one of the two forms, *dubius*, copies *Amauris psythalea damoclides* Stand., while the model of the other form, *anthedon* Doubl., is *Amauris niavius niavius* L. (Family Danainae). (The reader is referred to the condensed taxonomy

TABLE 1

Lepidoptera

(*after Kükenthal, 1936*)

Superfam. Rhopalocera (Butterflies)
fam. Pieridae (whites)
subfam. Pseudopontiinae
" Dismorphiinae, e.g., *Dismorphia*
" Pierinae, e.g., *Pieris*, whites, *Colias*, yellows
fam. Papilionidae (swallowtails)
subfam. Baroniinae
" Papilioninae, e.g., *Papilio*, swallowtail
" Teinopalpinae
" Zerynthiinae
" Parnassiinae, e.g., Apollo butterfly
fam. Lycaenidae 2 subf. (blues, etc.)
fam. Rhiodinidae 2 subf.
fam. Nymphalidae
subfam. Danaidinae (almost all tropical)
tribus Danaidini, e.g., *Amauris*, *Euploea*, and monarch butterfly
tribus Tellervini
tribus Ithomiini, only neotropical, e.g., *Mechanitis*, *Ithomia*
subfam. Satyrinae (meadow browns, etc.)
5 tribus
subfam. Nymphalinae
tribus Acraeini, tropical, e.g., *Acraea*
tribus Clothildini
tribus Heliconini, neotropical, e.g., *Heliconius*
tribus Nymphalini, e.g., *Argynnis*, fritillary

of butterflies in Table 1, from which the relative systematic position of the groups mentioned here can be ascertained, together with the popular names of some typical species. Colored pictures are to be found in Haase's and Eltringham's monographs, Punnett's book and in Seitz's standard work.)

2. Only one type of male exists, it being non-mimetic. There are two types of females; either, one resembles the male and the other is mimetic, or both types of females are mimetic. Examples of the former are found in this country. The swallowtail *Papilio glaucus* L. has in its southern range a second female form of dark color which is supposed to mimic *Papilio philenor* L. The type form is called *turnus*, the mimetic one *glaucus* (see fig. 1). The second type is represented by the African *Hypolimnas misippus* L. (Nymphalinae) where both types of females are mimetic; the female form *misippus* mimics *Danais chrysippus*, the other, form *inaria*, copies the *dorippus* form of the same model (Danaidae). In both cases the males, and, in the first example, the male-like non-mimetic females show the typical pattern of their group, which is very different from that of the model's group. This is also true of all other comparable cases to be mentioned.

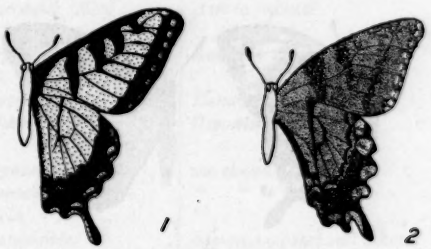


FIG. 1. PAPILIO TURNUS

1. ♂ (like non-mimetic ♀), ground color yellow.
2. mimetic ♀ *glaucus*, ground color except in wing margin blackish.

Illustrations in black and white are rather unsatisfactory; they are not meant to replace colored figures but to serve as a crude help to the reader who does not know the actual specimens.

3. Only one type of non-mimetic male exists. There are at least three types of females: either, one like the male, non-mimetic, another different and non-mimetic, and a third mimicking a different species; or, there is one non-mimetic female with the same pattern as the non-mimetic male, and two different types of mimetic females, mimicking completely different species; or, all females are mimetic and mimic different models. The best studied and most frequently quoted examples of this type belong to the swallowtails (Papilioninae). One typical example is *Papilio memnon* L. of Java, with many female forms. Those used for analysis (Jacobsen and De Meijere) are the form *laomedon* Cr., non-mimetic and like the male; *isarcha* Seitz (formerly called *agenor*), also non-mimetic but different; and *achates* Sulzer, which mimics the protected *P. coon* F. In this case it is rather remarkable that the non-mimetic forms and the males are tailless, while the mimic has tails

like the model. A second comparable case is that of *Papilio polytes* Fabr., from Ceylon. One of the females resembles the male and is non-mimetic (*cyrus* Fabr.). The two other female forms are here mimetic. The form *polytes* copies *P. aristolochiae* Fabr., and the female *romulus* Cram mimics *P. hector* L. In this case all forms, including the model, have tails. It is to be noted that in this group the models belong to the same genus *Papilio*, but to a different section, namely Pharmacophagi or feeders on poisonous plants. (According to Haase (1891–93) Papilios fall into three groups: Pharmacophagi or poison eaters, who frequently possess warning colors and furnish the mimicry models; Cosmodesmus, which only in South America mimics poison eaters; and Papilio proper, which provides mimics of poison eaters as well as of completely different groups.) One of the most beautiful examples of South American mimicry is provided by *Papilio lysithous*, with six mimetic female forms (Jordan, 1911); but here no genetical data are available (see below).

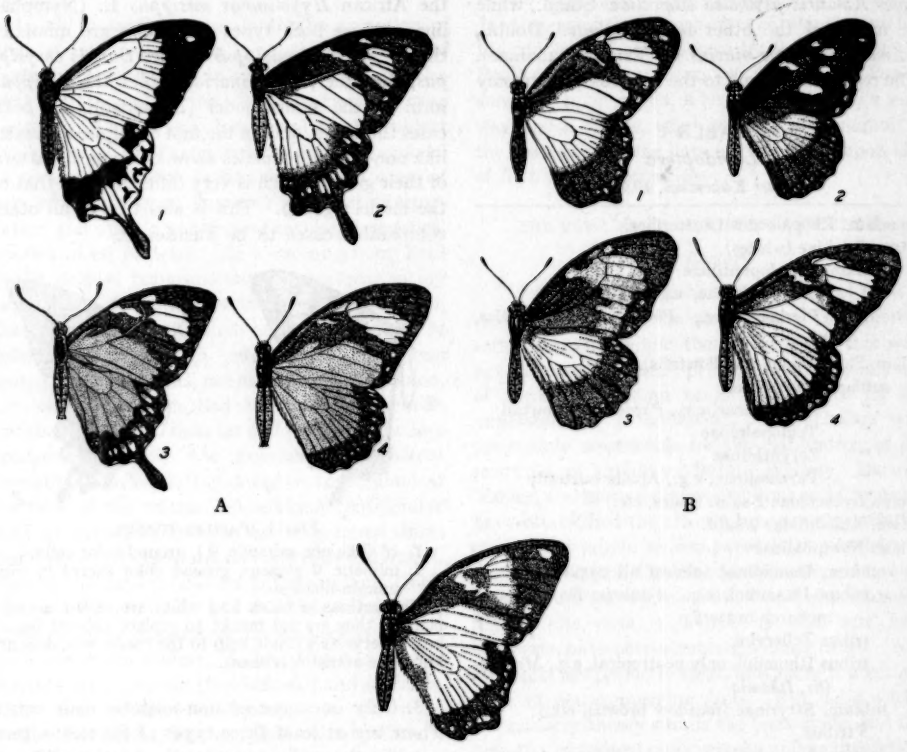


FIG. 2. SOME OF THE IMPORTANT TYPES OF PAPILIO DARDANUS REDRAWN FROM COLORED PLATES BY ELTRINGHAM (1910)

A. 1. ♂ of *cenea*, also basic type of non-mimetic ♀, ground color yellow (fluorescent in ♂).
2. *P. antinorii niavioides*, "tailed mimic," ground color white.
3. *P. a. ruspinae* dto., ground color brownish, spots white.
4. *P. d. trophonissa*, ground color forewings white, hindwings brownish.

B. 1. *P. d. hippocoon*, ground color white.
2. *P. cenea cenea*, ground color hindwings yellowish (geogr. variety).
3. *P. d. planemoides*, ground color forewings brownish, hindwings white.
4. *P. d. dionysus*, not mimetic, ground color forewings white, hindwings yellowish.

C. *P. polytrophus trimeni*, proto-hippocoonides, ground color male yellow.

4. Again only one type of male exists. The females may contain different types in the different

races of the African *Papilio dardanus* Brown, which provides the examples for this group (see fig. 2). The females may be male-like, or different female types may be non-mimetic or mimetic and utterly different from the males; all female types to be found in some libraries as collected contributions from the Hope Museum, Oxford). We shall return repeatedly to the types of variability visible in this table, which is based only upon the data used by Ford for his analysis.

TABLE 2

Mimicry in Papilio dardanus

(*See Fig. 2*)

HABITAT AND SUBSPECIES	NON-MIMETIC FEMALES	MIMETIC FEMALES	MODELS
Madagascar: *meriones*	one, with tails, like male		
Abyssinia: *antinorii*	one, with tails, like male	1. *niavioides*, tailed 2. *ruspina*, tailed 3. *wienholti*, tailed	*Amauris niavius?* *Danais chrysippus?* *Acraea jodutta?*
West Africa: *dardanus*	one different from male, *dionysus*	1. *hippocoon* 2. *trophonissa* 3. *niobe*	*Amauris niavius niavius* *Danais chrysippus* *Bematistes tellus*
Central Africa: *dardanus?*	—	1. *hippocoon* 2. *trophonissa* 3. *niobe* 4. *planemoides* 5. *cenea*	see above " " " " *Bematistes pogei* and others? *Amauris echeria*
North Eastern Africa: *tibullus*	one, *leighi*, rare, not malelike	1. *cenea* 2. *hippocoonides* 3. *trophonius*	see above *Amauris niavius dominicanus* *Danais chrysippus*
South Africa: *cenea*	the same	the same	
Mountains in Kenya District: *polytrophus*	like incomplete mimics, rudimentary tails, some male-like yellow pigment. 1. *protocenea*, i.e. between ce. and male 2. *protohippocoonides* 3. *prototrophonius* 4. *protosalaami* 5. *protoplanemoides*	1 *cenea* 2. *hippocoonides* 3. *trophonius* 4. *planemoides* 5. *salaami?*	see above " " " " " " " "

may be different and mimetic or one type non-mimetic, the others mimetic. Also half-mimetic "pseudo" types are found. The models belong mostly to the groups Danainae and Acraeinae. Table 2 assembles a few of the types which were recorded by Ford, but the actually described forms are still more numerous (see Seitz, 1907ff., colored pictures in Punnett, 1915; Eltringham, 1910; Seitz; Ford, 1937; and many smaller papers from the Poulton school in *Trans. Entomol. Soc. London*,

C. Parallel geographic variation

The foregoing table shows already that in *Papilio dardanus* geographic subspecies exist in which not only the males are different, as expected in geographic races, but also the mimetic females are more or less different, as their names indicate. These geographic differences involve the following phenomena: (1) existence or non-existence of male-like females; (2) occurrence or non-occurrence of non-mimetic females; (3) occurrence of mimetic

females which copy in one region a model species not copied in another region; (4) occurrence of mimetic females copying the specific geographic variety of the model living in the region. In addition, different percentages of the respective forms are found in the populations inhabiting different regions. (Tables are found in Ford, 1937.) This parallels the well-known cases of other polymorphic species which have been discussed, more or less completely, in all modern books on evolution (see below). The most interesting feature is of course the parallel geographic variation of model and mimic. This phenomenon is also found in such other mimetic species as have not been mentioned thus far because less is known about them generally, and nothing about their genetics. It applies also to such mimetic forms as do not exhibit polymorphism. For the genetic analysis these are useless and have therefore not been mentioned thus far. Yet some of the most perfect examples of imitation belong in this group, e.g., the South American Pierid ("white") *Dismorphia praxinae* which copies the red and black striped (warning color!) Ithomiine *Mechanitis saturata* (see Punnett, 1915, plate X); the swallowtail *Papilio pausanias* copying the conspicuous Heliconine *Heliconius sulphurea* (Punnett, plate XI); or the amazing group of Asiatic cases like *Papilio clytia* and *xenocles* or the White *Pareronia ceylonica* copying Danaids of the most characteristic design (Punnett, plates I–III; other illustrations in color in Fisher, 1930; Haase, 1891–1893; Seitz, 1907 ff.).

D. Parallel behavior of sexual dimorphism

In the cases mentioned thus far, either both sexes are mimics and more or less identical or only the females are mimics of other groups without sexual dimorphism. Still more remarkable are the rare cases in which both mimic and model are sexually dimorphic, and the same dimorphism is found in both. Punnett (1915) mentions only two such cases. One is that of *Euploea mulciber*, a model of the Euploeine family, in which the male is brown with a deep blue suffusion, while the female is lighter, with less blue, and light streaked hindwings. A satyrid mimic of this, *Elymnias malelas*, has a similar sex difference! (pictured in Punnett, plate II). *Papilio paradoxus* mimics the same *Euploea* in the same way! These rare cases are important, as is the whole subject of sex related to mimicry. This will be discussed below.

The taxonomic names used in our presentation are those used by the authors to whom reference is made. Frequently they are not the names approved by the rules of nomenclature. The proper names may be obtained from Seitz. Names quoted from Ford, however, have been checked by this author.

E. Mimicry rings

Another important group of facts which has played a considerable role in evolutionary discussions is found in the so-called mimicry rings. This term means that there are species which serve as models not to one but to different species of different groups. Punnett (1915) illustrates a convincing case in colors (plate IV). The ring contains two species of Danaids (in this case both sexes) supposed to be distasteful, namely *D. chrysippus* and *plexippus*; further, the female of the Nymphaline *Hypolimnas misippus* (the male being very different); further, the females only of the Satyrine *Elymnias undularis* and of the fritillary *Argynnis hyperbius*, the latter two being considered as unprotected except by mimicry. Parallel cases are quoted in the writings of Poulton, Carpenter, *et al.* But decisive proofs are not always available of the occurrence of the prerequisites for mimicry (identical distribution, similar habits, etc.) in such cases.

F. Variability of mimics

In the theoretical discussion of the origin of mimetism the variability of mimics plays an important role, first, in regard to ecological relations and geographic coincidence of mimic and model, second, in regard to the phylogenetic origin of the protective pattern. We shall discuss many details below. Data concerning the descriptive facts are found in the papers already cited and in many others containing descriptions of so-called intermediate or primitive forms. Many of these have been given special names which can be found in the monographs of Seitz' opus. In this paragraph we record the facts only as a whole, not going into the details of pattern. The most conspicuous aberrations from the mimetic pattern are expected where the mimics imitate a very different form and therefore are very much different from the male form, which is generally supposed to represent also the original female form. The most important set of data is available for the African *Papilio dardanus* (fig. 2), data which have been assembled and extended by Ford (1937), who could use the huge material brought together by Poulton as well

as that found in the great collections in England. As these data are an important link in Ford's discussion of the subject, we feel sure that he presented the facts rather completely.

1. Among the series of mimetic forms of *P. dardanus dardanus* is one, *dionysus* (see fig. 2b, *4*), which is considered to be non-mimetic. It has been described as either an intermediate between the mimetic female *hippocoon* and the non-mimetic female *meriones* or as a "reversal to an ancestral form." This type (to be discussed below) is considered to be very rare, not mimetic, and the black markings on the forewing vary from an almost male-like form to one nearly the pattern of the mimic. Another "rare nonmimetic form," in the subspecies *P. dardanus tibullus* and *P. d. cenea*, is the form *leighi* which combines some of the characters of the mimics *cenea* and *hippocoonides* with the mimic *planemoides*; the pattern of the forewing is somewhat variable (see fig. 2).

2. In the subspecies *P. d. polytrophus*, occupying the high mountain regions in the center of Tanganyika territory and parts of Kenya colony, an imperfectly developed mimicry is a typical feature. We shall discuss later Ford's explanation, which we state here in his own words: "Owing partly to the rarity in these mountain districts of the species which serve it as models elsewhere the various female forms so constant in other areas, are here exceedingly variable. Indeed they often show an approach to the ancestral male like forms." These imperfectly mimetic forms are distinguished by Poulton (1906), whom Ford follows, as "proto"-forms, independent of variety names given by taxonomists, e.g., proto-cenea including all varieties which may be described as imperfect *cenea* (see below and figs. 2, 9, 10). A proto-cenea looks like *cenea* but has the typical male yellow pigment which is absent in all typical mimetic females; proto-hippocoonides is intermediate in its black markings between the male-like female and the mimic *hippocoonides*, while male yellow pigment is usually present; proto-trophonius is more or less intermediate between the male type and the mimic *trophonius*. The black pattern varies as in proto-hippocoonides and white patches of *trophonius* are here male-yellow; *salaami* is a *trophonius* type in which white is replaced by orange to reddish brown; proto-salaami more or less resembles *salaami*, but the black pattern may be increased or considerably decreased and replaced by reddish ground. These types are considered to be non-mimetic. Proto-planemoides has a similar relation to *planemoides* as far as the black pigment is concerned. In this description of the proto-forms minor variations are omitted, such as yellow, fulvous, or white color of fore and hindwing spots (see below.) Collections from the district mentioned above include, according to Ford's count, 38 per cent of these proto-forms. *It is important to add that some of these abnormal forms occur as rare abberrations in other regions!* (For details, see Table 4.)

G. Genetics

It caused quite a stir among geneticists when De Meijere (1910) published the first genetic analysis of mimetic polymorphism in *Papilio memnon*, based upon Jacobsen's breeding results. This was a case of a *Papilio* in Java with one type of male and three types of females, one nearly like the male, and one of the other two copying a species of the Pharmacophagus group. In the original nomenclature the male-like female is called *laomedon* Cr., the non-male-like, non-mimetic female *agenor* L. (according to Ford it ought to be called *isarcha* Seitz) and the mimetic female *achates* Sulzer which copies the Pharmacophagus *P. coon* F. In this case all forms, including the male, are tailless except *achates*, which is tailed like the model. De Meijere realized that the breeding results can be explained on the assumption that all three female types are controlled by simple Mendelian differences. His detailed Mendelian explanation is now obsolete. The present author proposed (Goldschmidt, 1912) a somewhat different formulation which put the sex-controlled inheritance in the foreground and explained the situation as based upon two mutants of the alleles controlling the secondary sex-characters. A much simpler and now generally accepted formula was proposed by Baur (1911), which requires (in addition to sex-controlled inheritance) one dominant factor *A* which converts the female *laomedon* into *agenor* and a second factor *B*, which in presence of *A* produces the *achates* type.

Soon afterwards Punnett's student Fryer (1913) analyzed another case, that of the Ceylonese *Papilio polytes*, and he rather safely established the simple Mendelian relations between the forms. Following the old formulations of the Bateson school he represents the sex-controlled inheritance in terms of specific inhibitors, *Ii*. But I had already shown (Goldschmidt, 1912) that this type of heredity (the term sex-controlled was introduced only later by Goldschmidt, 1920b) is nothing but

ordinary Mendelian heredity under control of the respective sex and its specific physiology of development. The specific inhibitors are thus superfluous. We remember that in *P. polytes* one type of female (*cyrus* Fabr.) resembles the male, another, *polytes*, mimics *P. aristolochiae* and a third, *romulus*, mimics *P. hector* L. The breeding results were explained satisfactorily by a dominant factor *A* which converts *cyrus* into *polytes*, and one *B*, which only in the presence of *A* converts *polytes* into *romulus*. Table 3 gives the formulae for all types of individuals.

Among the simple cases, with only two forms involved, some breeding experiments are available. This applies to *Hypolimnas dubius*, reported above as a form in which no sex-controlled inheritance is involved. On the basis of the breeding results obtained by Lamborn and Platt, Carpenter and

TABLE 3

Genotypes of forms of Papilio polytes

MALES ALL ALIKE	MALE-LIKE FEMALE CYRUS	MIMETIC FEMALE POLYTES	MIMETIC FEMALE ROMULUS
aaBB	aaBB		
aaBb	aaBb		
aabb	aabb		
AaBB			AaBB
AaBb			AaBb
Aabb		Aabb	
AABB			AABB
AABb			AABb
AAbb		AAbb	

Ford (1933) conclude that one of the mimetic forms, *dubius* or *mima* (geographic races) is produced by a single Mendelian dominant from the other (*anthedon*).

What genetic knowledge is available regarding *Papilio dardanus* is mainly based upon the initiative of Poulton, who encouraged entomologists and fanciers residing in Africa to perform breeding experiments. Many individual reports have been published from the Hope Museum, some beautifully illustrated (mostly in *Trans. Entom. Soc. London*). The only geneticist to work over this material, much of which is preserved in the collections of that Museum, is Ford, whose detailed report (1937) we are therefore following.

The late Professor Poulton had, about twelve years ago, kindly granted me the permission to come to Oxford and to analyze his material; political events prevented me from taking advantage of his generosity. Fortunately Ford could still perform the work in Poulton's lifetime.

One of the basic difficulties emphasized by Ford is that most families were raised from captured females who might have been fertilized by more than one male. In addition the numbers look as if breeding was rather difficult and produced only small families, so that there is the possibility of differential mortality. The results cannot be summarized simply, as in the other cases. Actually, in the individual families obtained it cannot be decided with certainly which forms are dominant or recessive. Ford constantly had to refer to the percentages found in nature, which frequently do not fit properly the genetic results. Thus a detailed review is of not much use. The only statement which can be made is that, as far as the data go, one must expect a similar Mendelian situation for the major forms to that found in other polymorphic Papilios, as the families either consist of one or of different forms in what looks like Mendelian ratios.

It should finally be mentioned that there are indications of lethality or semilethality of homozygous dominants, (Carpenter and Ford) a fact observed also in other non-mimetic cases of sex-controlled inheritance by Gerould (1921) and by Goldschmidt and Fischer (1922). Ford is much interested in this point from the standpoint of selection in populations and discusses it in a recent contribution to *The New Systematics* (Huxley, 1940) (see below).

THE ORIGIN OF MIMICRY: PUNNETT VS. FISHER

Bates, Wallace, Darwin, and their successors Müller, Haase, Weismann, Marshall, and many others down to Poulton, discussed the origin of mimicry in general and of the special type which is under scrutiny here, from the standpoint of evolution by selection of small aberrations.

I should like to pay tribute to the memory of a great naturalist by mentioning that my interest in the subject was first roused when, as a young student (in 1901) I had the privilege to listen to a brilliant exposé of the subject by Professor Poulton.

Darwin himself did not fail to see the difficulties arising from the fact that selection can only work when a sufficient amount of resemblance between mimic and model has already been accomplished, sufficient to deceive the enemies. The genetic discoveries that such great differences as those

between non-mimetic and mimetic females are based upon simple Mendelian factor differences suggested to Punnett a review of the whole subject.

Punnett (1915) first stated the case for warning coloration of distasteful forms and its imitation by mimics, as first observed by Bates in South America and therefore called Batesian mimicry; the classic models were later found by Wallace in Asia and by Trimen in Africa. Müllerian mimicry, i.e., mimicry between two distasteful forms, is treated as a special case. This, however, does not concern us here. After a detailed description of the best known cases of mimicry (a review which, together with Haase's classical work, 1891–93, can be recommended as a fair summary of the facts) Punnett offers his criticism of the classical theory of the origin of mimicry by gradual selection. Some of this criticism applies to the basic characteristics of any mimicry, as stated first by Wallace, i.e., occurrence of both forms in the same locality, harmless nature of the mimics, smaller numbers of them, considerable difference between the mimics and their next relatives, and purely external character of the similarity. Cases are mentioned which do not agree, and some of the rather wild explanations offered for aberrant facts are held up to ridicule. To mention only a few: The fritillary *Argynnis hyperbius*, supposed to mimic *Danais plexippus*, lives in the mountains while the model lives in the plains. The flight of such mimics as *Papilio clytia* or *Hypolimnas misippus* is completely different from that of their models of the Danaine and Euploeine group, and the same is true for non-mimetic as well as mimetic females of *Papilio polytes*. The mimics are not always completely different from their non-mimetic relatives, and the amount of difference found within the non-mimetic group is not smaller than that between mimic and model. In spite of such discrepancies the fact of mimicry is considered as established. But some of these discrepancies will enter the discussion of the origin of mimicry.

In the discussion of the origin of mimicry Punnett stated at the outset the two major possibilities: Either the resemblance has been brought about through the gradual accumulation of small variations by selection, or the mimetic form originated as a sudden mutation, and selection is responsible for its survival and for the destruction of the less adapted form. Fisher later called the second view origin by "saltation" and we shall therefore henceforth distinguish the two theories as the Darwinian or neo-Darwinian theory and the saltation theory.

The term saltation describes properly a large mutational step. I have spoken elsewhere (1940) of systemic mutation which however, implies a definite interpretation, namely intrachromosomal changes of a more complex nature than in ordinary mutation. Dobzhansky, in a critique of my views, has called them, unfortunately, a cataclysmic theory and this word has been repeated since by others as a kind of slighting label for unwelcome ideas. Cataclysma means deluge or catastrophe and thus does not convey the meaning of something involving only larger-sized causes and effects than assumed usually, but rather of something irrational and damnable. I must therefore object to the designation cataclysmic theory.

The first difficulty of the Darwinian theory, which was well known to Darwin himself, is the problem of the first step. If this does not produce a sufficient similarity with the model to deceive predators it has no selective value; but how can a small variation achieve such a minimum resemblance? Darwin and Wallace overcame this difficulty by assuming that originally there was only a small difference between mimic and model and that afterwards the present type was simultaneously built up in both. A powerful argument (already realized by Darwin) against this view can be derived from the so-called mimicry rings.

As already mentioned, it happens "that a given species in a given locality may serve as a model for several other species belonging to unrelated groups." In such a ring palatable and presumably unpalatable forms may be united. If now the Darwinian explanation of a slow accumulation of variations toward the warning pattern in both model and mimic, originally not very different, is applied, it follows that the ancestors of the members—e.g., one ring from Ceylon specified by Punnett as a Danaine *Danais plexippus*, a Nymphaline *Hypolimnas misippus* (here only the female is involved), a Satyrine, *Elymnias undularis* and a fritillary, *Argynnis hyperbius*—have been more or less alike. Such an idea would hardly appeal to anybody. This is still less the case if the sexual differences are also taken into account. Thus Punnett does not see any solution of such cases except by the saltation theory. He is also opposed to an intermediate view, that by a single mutation first a rough-hewn resemblance is brought about that is later perfected by selection of small variations. In his opinion this requires that selection continues operating, because otherwise

the likeness would gradually deteriorate by regression. This is not considered to be the case.

Punnett's major argument is however derived from the case of *Papilio polytes*. Here quite a number of discrepancies in distribution, mode of flight, distinguishability of model and mimic have been observed. But here also the genetic analysis showed that simple Mendelian differences are responsible for the different types of females, as reported above. As such differences are only known to arise by single mutations, the mimetic resemblance must have been brought about in a single step for each type. (*It ought to be emphasized that neither in P. polytes nor in memnon was a single intermediate form found in the rather extensive experiments.*) Thus selection had nothing to do with the origin of mimetic resemblance though it probably worked in conserving it. Punnett discusses the latter point in detail, using the Hardy-Weinberg formula (see Stern, 1943, for this designation) for testing expectations in a population; in view of the persistence of a large percentage of the non-mimetic females over hundreds of generations, as judged from collectors' data, Punnett doubts that the mimics have much of a selective advantage. He mentions in this connection the case of industrial melanism, to which we shall return below, and also discusses the facts about the enemies of butterflies with which we are not concerned here, as our discussion presupposes the reality of mimicry.

Another important problem is discussed by Punnett: Even if mimetic forms originate by saltation, to use Fisher's term, selection will prevent establishment of new variations away from the mimetic resemblance. But in the absence of selection the resemblance will slowly be diminished or completely lost, an idea applied to actual cases especially by Carpenter (1913). Carpenter's famous example is that of the Nymphaline *Pseudacraea eurytus* mimicking the Acraeine genus *Planema*. On the mainland of Africa (Uganda) three mimics are found imitating perfectly three species of *Planema*, the latter being more abundant than the mimic in agreement with Wallace's rule. On Bugalla Island, however, the models are rather rare and the mimics abundant, and here many more transitional forms (as illustrated in many photographs) are found than on the mainland. (The parallel case of *P. dardanus* will be discussed below.) In this case little of the genetics is known except that different forms can be derived from eggs of captured females which makes it probable that the genetical aspect will not be much different from the cases already studied. Punnett suggests that the intermediates are heterozygous in some factor for which the typical form is homozygous, which would explain simultaneously the large number of intermediates in the population. The last word would be left to a future genetic analysis.

Punnett finally discusses some of the facts relating to parallel geographic variation. He does not enlarge upon such cases, as mentioned above, in which well known models and mimics show a parallel geographic variation. He uses, moreover, as an example a group of South American butterflies with warning colors which might constitute a mimicry ring or might not. Whether mimicry is involved or not, the fact remains that a series of "species" (probably subspecies or geographic races according to present-day notions) exists in different localities which show typical differences in pattern; and these differences run completely parallel in members of the families Heliconinae and Ithomiinae (more details below). Punnett makes the suggestion (since proven to be correct in other cases of geographic variation independent of mimicry, e.g., by the present writer for *Lymantria dispar*) that the new color scheme was associated with some physiological peculiarity which was advantageous to the individual in its new surroundings and was therefore selected. The same thing could happen in a parallel way in different species. (Again known to be the case in other groups, as the much discussed rules of Bergmann, Allen, Gloger, etc., in mammals and birds prove; see discussion below.)

In drawing his conclusions Punnett introduced still another genetical interpretation. He started with the fact that cases of mimicry tend to run in series, i.e., that a closely related series of mimics tends to resemble a closely related series of models, e.g., in Africa Papilios of the Cosmodesmus group mimic Danaid and Acraeid series. Thus the majority of cases of mimicry belong to one or another of such series as mentioned. "The natural interpretation of such phenomena" (Punnett) would be that in each group of Lepidoptera involved certain pattern factors are present, the permutation of which would produce the variety of patterns. Some of these factors (genes) may be common to two or more groups and thus make for similar patterns of unrelated forms. As a parallel case the coat color genes of different rodents may serve (Punnett); one could actually say that in

some respects the rabbit mimics the mouse, in other features the guinea pig. With such a parallelization agrees the fact (always according to Punnett) that widely different models of different mimetic females of a species are related among themselves; it does not occur that one female form mimics a Danaine and another a poison-eater *Papilio*. If the explanation thus offered is correct, there would be available, among the possible pattern permutations of one group, combinations resembling those in another protected group. In this case a simple mutation of the basic color (e.g., harmless white into warning red) would at once produce the mimetic resemblance. But Punnett does not tell us how this scheme, which works theoretically between one *Papilio* and one *Danais*, etc., could be applied also to cases with three different kinds of females of completely different patterns.

If I am not mistaken, not many *geneticists* discussed the problem of the evolution of mimicry at that time, taking sides for or against Punnett. Actually the problem, one of the oldest and most important in evolution, is not even mentioned in such recent neo-Darwinian books on evolution as the excellent treatises of Dobzhansky and Mayr, though Shull, in his text (1936), largely follows Punnett, as far as genetics is concerned and goes even beyond him in his general criticism of mimicry (see Shull, 1937, vs. Carpenter, 1937). The present writer tried to set this problem into a definite place within his ideas relating to genetics and evolution and asserted (1920a) that the general trend of Punnett's ideas could hardly be refuted, though some points in detail require reconsideration. It was R. A. Fisher (1927, 1928, 1930) who took up the problem again from the Darwinian point of view in some papers preliminary to his well-known book, a work which is, to a large extent, responsible for the upsurge and present prevalence—almost a fashion—of neo-Darwinism.

Fisher was led to this problem by his well-known theory of the origin of dominance by selection of modifiers in the heterozygote. His basic concept is that selection acts upon the gene complex, modifying the response of the organism to the particular factor in question which itself remains unchanged. Rare genes will exist almost exclusively as heterozygotes. If they are disadvantageous, those individuals will be favored whose gene complex interacts to bring out the effects of the gene in question to the least degree, and vice versa in case of beneficial genes. Thus the tendency for characters to become dominant by plus selection of dominance enhancers (or to become recessive by the opposite selection) is spread through the species, while the existence of recurrent mutation allows repeated experience of genes acting in either direction.

One of the consequences of this idea is that the basic activity of a gene may be completely unaltered while selection acts upon modifiers for the phenotypic end effect. Statistically speaking, the selection of modifiers will be especially rapid in polymorphic forms because here the heterozygotes are still more plentiful than in the simple case. If this argumentation is applied to the facts of the genetics of mimetic polymorphism, the following explanation follows (Fisher, 1927): When any mutation produces by chance "*a remote resemblance*" to a more protected species, from which some advantage, however small, might be derived, the deception will constantly be improved by selection. This, working upon genotypical variability (i.e., on the whole residual heredity) will result in a gradual change in the effects of the gene concerned. Thus the effects will become very different from what they were at first. But the gene itself is unchanged and remains as a switch, turning on one or another set of characters subject to genotypic variability and thus susceptible to selection. Thus, though the forms of a species may be controlled by a single factor difference, which must have originated suddenly by mutation, we are nevertheless entitled to regard them as the product of slow evolution. (This review of Fisher's viewpoint has made use of literal excerpts from Ford, 1936, 1937.)

In presenting his idea of a switch mechanism, Fisher (1927) uses sex determination as an illustration, a comparison which Ford (l.c.) and Huxley (1943) accept. Fisher argues: "The core of Punnett's argument in favor of the production of mimetic forms by saltations lies in the Mendelian behavior of the polymorphic females, for it is argued that these Mendelian factors must have arisen originally as mutations, and seeing that the different forms demonstrably differ by only single factor differences, these types must have sprung into existence each at a single leap. Convincing as this argument at first sight seems, we should, nevertheless, at once recognize our folly if we argued that because the sex difference in *Lebistes* is apparently determined by a single factor, therefore a female fish of that genus with the appropriate adaptations of her sex had arisen by a single saltation from a male of the same species! [*Sic!*] Or

vice versa. In this case we are freed even from the necessity of rejecting the supposed saltation as improbable, for since the reproduction of the species requires the cooperation of both sexes, we may be certain that the origin of the sex factor antedated the evolution of separate sexes, and has persisted, in its function of switch, unchanged during the whole course of the evolutionary development of these two types. The example of sex emphasizes strongly the fact that it is the function of a Mendelian factor to decide between two (or more) alternatives, but that these alternatives may each be modified in the course of evolutionary development, so that the morphological contrast determined by the factor at a late stage may be quite unlike that which it determined at its first appearance. The inference (on mimicry) requires, in fact, the gratuitous assumption that no evolutionary change has taken place in the two alternative forms since the dimorphism was first established."

Another comparison used by Fisher is that with the inheritance of pattern in hooded rats. The hooded pattern is a simple Mendelian recessive to self color. But a series of modifiers control the amount of color from almost dark to almost white by extension or restriction of this pattern, and these modifiers can be selected, thus producing selection of plus and minus patterns (Castle, 1919). Fisher ends this argument by saying that "unless the above analogies are wholly misleading" the alleles *A* and *B* (or *H* and *R* in Fryer's terminology) in *P. polytes* can be supposed to have arisen by mutation and remained what they were; but that there is no reason to believe that the combinations *AAbb* or *AABB* resembled at their first appearance the present types of swallowtail of these formulae. The selection of modifiers produced the mimetic types only afterwards. Once produced they are kept up in definite ratios because such stability is based upon the selective advantage of the actual ratio of the alternative types. Different such stabilizing actions are possible, one of them being reproductive selection of lethality of certain combinations (both of which have been observed, the first in *P. polytes* by Fryer (1913), the second in cases of sex-controlled dimorphism without mimicry by Gerould (1921) in *Colias* and by Goldschmidt and Fischer (1922) in Argynnis).

In a number of publications (1936, 1937, 1940a, b) Ford took up the problem of polymorphism and fully accepted Fisher's ideas. He added some new arguments based upon his own work, the most important of which are the following:

Fisher's use of the example of the hooded rats is followed up by a study of comparable genetic situations in Lepidoptera, which are used for a comparison with the mimicry cases. Ford himself (1940) studied crosses between *Abraxas grossulariata* (currant moth) and a yellow variety *lutea* distinguished by a simple Mendelian factor. F_1 is more or less intermediate and F_2 segregates in a bimodal curve. By selection it is possible to shift the degree of color in the heterozygote as well as in the homozygote. This must be due to the presence of modifiers which influence the phenotype within an ordinary monohybrid segregation. The selective change in the heterozygote may, of course, also be described as a shift in dominance in agreement with Fisher's view. (In *Drosophila* dominance modifiers are well known and have been made the subject of a special analysis by the present author under the name of dominigenes, see Goldschmidt, 1938a.) The parallelism to Castle's hooded rats is self-evident. As another example Ford quoted Federley's work (1920) on *Spilosoma lubricipeda* and its melanistic geographic race *zatima*. The heterozygote is intermediate, but by selection of modifiers it can be shifted in both directions. The homozygotes show much less effect of the modifiers than the heterozygotes, a fact which Ford considers important from the standpoint of Fisher's theory of dominance. (Details will be discussed below.) Both these examples are used as a genetic comparison upon which to base Fisher's explanation of mimicry.

In Ford's discussions the existence of intermediates between the mimics and non-mimetic females of different mimetics plays a considerable role. Actually he considers this phenomenon as a potent proof of Fisher's theory. Thus we learn of the case of *Hypolimnas misippus* L., where two types of females copy *Danais chrysippus* and *dorippus* respectively. The two mimetic females (*misippus* and *inaria*) are based upon an unifactorial difference, as already stated, *inaria* being recessive. Rare intermediates between them occur in nature and Leigh (quoted from Ford) bred from one such. He obtained a family of 8 females (sic!) of which 4 were *misippus*, 3 *inaria*, and 1 intermediate. From this Ford concludes that the intermediates have a genetic basis and adds: "Here then is an instance of genetic variability within the expression of a single gene in a

mimetic species. It is of precisely the type required by the theory. . . ."

Ford has made a special study of the intermediates in *P. dardanus*, where they are described (aside from the taxonomic names given to them by collectors) as "variability" of the main types or as "incompletely developed" forms. They appear as rarities in the different races mentioned above, but, as already reported, are rather frequent in one subspecies, *polytrophus* of the highlands around Victoria Nyanza. They are considered so important because in this region the models are supposed to be very rare. Therefore, it is assumed, selection for the mimics has more or less ceased, and thus the modifiers may change the type without selective punishment. It must be emphasized that here the incompletes are something different from the intermediates in the last mentioned example. "Indeed they show often an approach to the ancestral malelike forms. This may be recognized in three ways. First the amount of black pigment on the wings is often reduced. Secondly females with rudimentary tails are sometimes found. Thirdly they may possess a certain amount of the yellow pigment of the male, present also in the malelike females of subspecies *meriones* and the *antinorii* group, but never in the females of the other races. . . ." To this must be added that the male yellow pigment is fluorescent in ultraviolet light (Cockayne, 1924), while no other pigments, even of the same color, show this phenomenon. Some of these incomplete females have been described above (proto-trophonius, etc.). More details will be found in Table 4 (see also figs. 2, 9, 10).

There is relatively much information available on the genetics of these incompletes, though Ford states that it does not seem possible at present to draw definite conclusions, with one partial exception. It is fairly sure that all these forms are genetic and that they are inherited *on rather simple lines*. Each form appears significantly more often among the progeny of its own type of female than among those of the other varieties. It seems that the proto-forms are recessive to the full form, assuming that they are based upon genetic modification of the same allele. One result obtained from a controlled mating (which alone excludes mating with more than one male) is remarkable: A wild

TABLE 4

Incomplete forms of P. dardanus, compiled from Ford, 1937

(*See Fig. 2*)

TAXON. NAMES	LIKE INCOMPLETE FEMALE	PATTERN	PIGMENT
Swynnertoni Poulton *mixtus* Aur. (proto-planemoides)	*planemoides*	Orange bar on forewings interrupted by black	Base of hind wings pale yellow (instead of fulvous)
Dionysus Doubl. (only in *P. dard. dard.*)	*hippocoon*	Area on hind wings enlarged, black markings, forewings variable, sometimes reduced to almost male type	Area hindwings pale yellow instead of white
Proto-cenea	*cenea*		Some male yellow pigment
Trimeni Poulton, *dionysoides* Aur. together: protohippocoonides	*hippocoonides*	Intermediate to male-like females	± male pigment
Lamborni Poulton (proto-trophonius)	*trophonius*	Black markings forewings variable, orange area restricted	Male pigment in all areas white in *trophonius*
Poultoni Ford *dorippoides* Trim. (proto-salaami)	*salaami*	Black markings increased or decreased ±	Small spots in forewings yellowish or white (instead of reddish brown)

cenea female had produced 13 *cenea* and 7 proto-cenea. One *cenea* and two proto-cenea were mated with brothers. The first female produced 7 *cenea* and 1 proto-cenea; one proto-cenea produced 5 proto-cenea and 8 proto-trophonius; the other one produced 4 proto-cenea. (Ford thinks that the ratio 8:5 is significant for an expectation 3:1; but according to Warwick's tables it is highly insignificant for all ratios up to 15:1; the 7:1 ratio is insignificant for all possible ratios, and so is the 4:0 ratio. In my opinion no conclusions can be drawn from the ratios except that only two types are segregated.) The proto-salaami form gave rather comparable results, namely offspring: either only proto-salaami, or proto-salaami and *hippocoonides* in a significant 1:1 ratio, or proto-salaami and proto-trophonius.

There is finally one important result: *poultoni* is a small deviation from the proto-salaami type, but intermediates exist. A brood from such an intermediate contained all transitions between *poultoni* and proto-salaami, which, however, means only, judging from Ford's plate, small variations in the completeness of a dark band (see fig. 9).

"Intermediates" have also been recorded in other cases of polymorphic mimicry. Thus in the North American *Papilio glaucus* the yellow non-mimetic female (*turnus*) is supposed to be recessive (Cockayne, 1932) to the mimetic dark form *glaucus* (model *P. philenor*). But intermediates occur, and "these are probably due to a failure in dominance" (Ford, 1937).

It is to be noted that Ford, though emphasizing the importance of the intermediates and "incompletes," does not derive any detailed genetic conception concerning these forms. He states only on different occasions that "they (the intermediates) do, however, represent precisely the type of variation which we are here postulating as providing a basis upon which selection may bring about gradual evolutionary change."

A third major topic in Ford's argument against Punnett's theory of saltation is his criticism of Punnett's idea that the mimetic resemblance might be explained on the basis of parallel mutation (see above, p. 156). Ford emphasizes (with Fisher) that one of the most consistent features of mimicry is its superficiality (Fisher had mentioned different insects imitating ants and other such types of mimicry). Though the patterns of model and mimic may be extremely alike in their general appearance, they are nearly always distinct in their detailed marking, the similar colors seem often to be produced by different pigments or in a different manner. Thus Ford concludes (1937): "When we find apparent similarities between models and mimics constantly dependent upon devices of a fundamentally different kind, it is impossible to regard them as due to parallel mutation. It may also be mentioned that such a view necessitates a corollary which I believe few workers would be willing to accept: that the differences (e.g., in pattern and color) between dissimilar, and often not closely allied, species are themselves unifactorial if copied by a mimic exhibiting unifactorial polymorphism."

Ford believes that a powerful argument in favor of such views may be derived from his studies on the chemistry of wing pigments. He finds (1927, 1940) that red pigments in Lepidoptera are generally of two types: A, which is converted by strong mineral acids into bright yellow and returns to red in alkali; B, which turns into dull bluish after treatment with acid. It turned out that the models of the Pharmacophagus group in the swallowtails have pigment A while the mimics have B (e.g., in the *P. polytes* case).

Finally, it may be mentioned that Ford offers also an interpretation of the fact that frequently mimics copy the specific geographic form (subspecies) of the model characteristic for different regions. (Examples have been mentioned before.) Without going into details Ford asserts that it may be supposed that selection, operating on the gene-complex, has adjusted the effects of the same factor to the needs of the different races.

Thus Fisher's and Ford's arguments against Punnett's interpretation may be summarized in telegraphic style: 1. Intrinsic improbability of sudden emergence of the mimetic pattern. 2. Availability of a neo-Darwinian conception of evolution by selection of modifiers (derived from Fisher's theory of origin of dominance). 3. The simple Mendelian basis thus would apply only to a switch reaction. 4. Genetic models for such a situation exist, namely inheritance of sex, of color in hooded rats, and some examples in Lepidoptera. 5. The relative numbers of mimics and models agree with selectionist expectations. 6. These expectations agree with facts indicating a greater variability of mimics where models are rare. 7. Parallel geographic variability is best explained by selection of modifiers. 8. The existence of intermediates is a proof of the presence of many otherwise invisible modifiers. 9. An explanation via parallel mutation in mimic and model is excluded because the

similarity is only superficial, e.g., different chemistry of pigments.

DISCUSSION AND CRITIQUE

Fisher attributed considerable general importance to his analysis of mimicry, as the following quotation (1930b, p. 147), as well as the printing of two colored plates, shows: "It will be clearly understood, from the argument of chapter one, that in the opinion of the author the bearings of genetical discoveries and in particular of the scheme of Mendelian inheritance upon evolutionary theory, is quite other than, and indeed opposite to, that which the pioneers of Mendelism originally took it to be. These were already, at the time of the rediscovery of Mendel's work, in the full current of that movement of evolutionary thought, which in the nineties of the last century has set in in favor of discontinuous origin for specific forms. It was natural enough therefore that the discontinuous elements in Mendelism should, without sufficiently critical scrutiny, have been interpreted as affording decisive evidence in favor of this view. *Nowhere perhaps in biology has this current of opinion introduced such serious discrepancies as in the interpretation of mimetic resemblance.* (Italics added.)" It is surprising that, in view of such evaluation, the problem has been discussed so little. Ford, a former student of Fisher, and Huxley, also Ford's former teacher, have accepted wholeheartedly Fisher's interpretation, as has also Carpenter. The present author, who had accepted Punnett's viewpoint formerly (1920, 1927) still clung to it in a recent book (1940); also Shull (1936) followed Punnett in his text on evolution. It has already been mentioned that such modern texts as Dobzhansky's and Mayr's do not even mention the problem.

A rather extensive discussion, not only of polymorphic mimetism, but of the entire subject has been presented by Nicholson (1927). He also accepts Punnett's views for such cases as the Papilios but demands slow selection of mutations for types of mimicry like similarity between beetles and ants. In the former cases he is ready to accept Punnett's views because the pattern systems of different families of butterflies are basically not different, and he proposes also a developmental explanation similar to one proposed by the present writer. We shall return to this point.

The most detailed recent discussion of the subject is found in Robson and Richards' book (1936). Their standpoint is more or less one of *non liquet*. Thus they state after presenting Punnett's and Fisher's views: "It may be noted that there is no *more* evidence for this theory (Fisher's) than there is for the simpler assumption (Punnett's)." They criticize especially the incompleteness of the factual data regarding variability, geographical distribution, ecology, and genetics, and emphasize the difficulties of the selectionist interpretation. They summarize their conclusions thus (p. 260): "The fact of mimicry, of striking resemblance between structurally unrelated forms, is well established, and the phenomenon is widespread, especially among insects. In a number of selected examples there is a considerable degree of probability that selection of warning patterns has brought about colour convergence. In another series of examples it is very difficult to see how selection could have led to the observed effects. In the majority of cases of mimetic resemblance, however, it is impossible at present to estimate to what extent, if at all, selection has been active. We are left, in fact, in a state of suspended judgment: it is probable that selection has played some part in the evolution of mimetic convergence, but it is normally impossible to say how large a part in any particular case." Later on they declare that it is certainly dangerous to use the mimicry theory as one of the main lines of support to the Natural Selection Theory. Another English geneticist, Watkins, has recently (1935) come out in favor of Punnett's viewpoint, without presenting a detailed discussion.

In view of the evolutionary importance of the problem I propose to inquire in detail into the entire body of relevant facts, omitting only the whole set of evidence in favor of mimicry itself, which I consider, with most biologists, an established interpretation.

A. Some general features

At the basis of all problems of adaptation, and especially of the origin of mimicry, lies the old question: how did the adaptation start? Darwin and Wallace (see above, p. 154) already realized the basic difficulty for slow evolution of mimicry, namely the first beginning. This must have had sufficient selective advantage to begin with, in order to be available for further natural selection. Darwin clearly believed that a small variation in the direction of the model did not suffice to start the ball rolling and therefore devised the idea that, at that time, the models were not very different from

the mimic. This idea did not find much favor later and hardly solved the problem. Therefore, Punnett insisted that the similarity must have arisen in one step to be effective, and neither he nor Nicholson nor the present author found any difficulties in imagining such an event. On the other side, Fisher (1930b), as well as Ford, considered this impossible: "... while on the contrary the assumption of discontinuity becomes a burden upon the theory, involving as it does the definite improbability of hitting off a good resemblance at one shot" (p. 163). In another place (p. 165) Fisher adds that the origin of resemblance by a single mutation requires "the gratuitous assumption" that no change has occurred since the first mutation originated. I think that this statement amounts to begging the question; why should a successful, i.e., well adapted mutation not remain stable if conditions remain the same? Ford (1927) even asserts that "the numerous instances of this kind make it impossible to believe that selection has had to wait upon the fortuitous occurrence in each of a mutation having the varied effects required. This would be an almost impossible conclusion even if a single species only had been involved." To this we might remark that the "fortuitous occurrence" has as much chance to happen as the initial mutation required by the neo-Darwinian theory provided that the proper developmental system is present. We shall develop this point below.

It is certainly of no use to discuss such statements of belief or disbelief made by both sides to the discussion, and we shall therefore have to look for more objective criteria. But a few remarks on the general attitude to be assumed toward the problem as a whole may not be out of place. Let us assume that we should find in nature a species of flies with two forms, one normal and one wingless; or one normal and one with four wings; or, one normal and one with four halteres; and further that genetic analysis shows that the two types are inherited as simple Mendelian differences. The neo-Darwinian would conclude that the origin of such huge departures (actually on a level of macro-evolutionary differences) could only be explained by gradual selection and accumulation of small modifiers. But actually these types are known to have arisen in the laboratory as single mutants in *Drosophila*. I should think that this example contains a warning to those who argue on the basis of a priori impossibilities. I cannot help feeling that in the case of mimicry the difficulty of the Neo-Darwinians to imagine an origin in a single step is based upon their a priori conviction that all cases of evolution *must* be explained by the selection of small deviations. Nobody, certainly, doubts that Fisher's theory of evolution of dominance by selection of modifiers is unassailable in principle. But this does not mean that every adaptation must be explained on the same basis. In passing judgment whether a definite type of evolution can be considered as possible or not we cannot trust our a priori disposition but must ask ourselves, as already stated, *whether the genetical and developmental system present in the forms under discussion permits or does not permit such a thing as evolution in one step.* We shall try to do this below.

There still remains, while discussing generalities, the problem of the first step as required by the neo-Darwinian explanation. The neo-Darwinian theory cannot work either before a resemblance of the mimic to the model is established which is at least so close that the predators are deceived, even if the similarity is not yet perfect. Thus everything is centered upon this initial step, which, if I understand it correctly, is assumed by Fisher and Ford to be due to a small mutation in the alleles *A* and *B* which we know to be the differentials that switch the pattern from non-mimic to mimic, in Fisher's language. This point seems to be generally passed over without much discussion. Fisher says that there is no reason to believe that, e.g., the *AAbb* form of *P. polytes* originally resembled much the present form *romulus* or was an "effective mimic" of *P. hector*. Ford speaks more concretely of any mutation which chances to give a "remote resemblance" to a more protected species, from which some advantage, however slight, might accrue. We must ask how remote the resemblance can be to have selective value. Can we really assume that the birds and monkeys and also mantids are such wonderful observers (or that some very clever ones among them are) to notice a "remote" resemblance and to be repelled by it? I think that this is asking too much. The minimum any selection theory of mimicry needs is a *fair* resemblance. But if we look at the actual specimens we realize that a fair resemblance would be not very much different from the present mimetic pattern. Therefore I cannot see why a mutant producing a fair resemblance cannot just as well produce a good resemblance.

There is another important point which is passed over in discussions. There exist cases in which both sexes are mimics. This shows that here the

male also profits from mimetic advantage. In the majority of cases, however, the males are non-mimetic. Did they not need protection which is only needed by the egg-laying female? Why, then, are some males mimetic? Or does the mechanism of sex-controlled inheritance prevent the modifiers from acting in the male? If so, why have not male sex-controlled modifiers been selected if the male also needs protection? In some instances there are found non-mimetic and mimetic females. One should expect the non-mimetic females to disappear. In *P. memnon* there are two types of non-mimetic females and one mimetic. Polymorphism is thus present in the same species with and without mimicry, but the modifiers of two non-mimetic forms are not counter selected against. At least we should expect the non-mimetic females to have that remote resemblance. It would not be difficult to invent some kind of explanation for these occurrences, as has been done by statistical deliberations. But it is difficult to see why the simple explanation which does not require new hypotheses from case to case is rejected. If the second non-mimetic female is a mutant, why not the third mimetic one? But let us not continue with such general argumentation but analyze the factual basis as well as the logic of the opposing theories.

B. The model of sex

In presenting his theory of selection of modifiers for a switch reaction of a mutant allele, Fisher takes the determination of sex as an example to make his point clear. His followers have accepted this model, and Huxley (1943) has even improved on it by stating more clearly the supposed parallelism. The idea is that in the case of mimicry recombinations of pre-existing modifiers as well as new mutations (modifiers) are selected, all of which depend for their expression on the presence of the original mutant which started the mimetic resemblance. Thus the original gene-difference acts as a switch controlling the action of numerous other genes "precisely as occurs in the case of the primary sex-difference in regard to genetically sex-limited characters" (p. 102). This sounds convincing at its face value, but the comparison cannot stand a closer scrutiny of the details. Let us first realize what we are asked to accept as the probable course of evolution of mimetic resemblance, for which the assumption of a similar situation in the evolution of sex is used as an illustration. There must have been present at the time of the first mutation of the "switch-gene" towards the "remote mimetic resemblance" a series of modifiers capable of changing the effect of that mutant, and some of the modifiers or some combinations of these were acting in a direction which, by chance, improved the mimetic resemblance. This involves the assumption that modifiers for all kinds of changes are always available for selection, therefore also those which by pure chance change the pattern towards that of the model. I note that this situation is not regarded as improbable, while a single "fortuitous" mutant (see quotation above on p. 157) is considered as highly improbable. These modifiers were slowly selected by the clever birds, monkeys, and mantids who could distinguish the small improvements towards the unpalatable model. Simultaneously other mutants appeared and were selected if they had the property of acting only in the presence of the switch-gene and, in addition, acted in the direction of further improving the mimetic pattern. (This requires, of course, that all other mutants could not compete.) In a case like *P. dardanus* or *polytes* a second switch-mutant (at least) appeared, and this whole process was simultaneously carried out for the second mimetic pattern. In addition, the two mutants must have acquired the dominance relations required by the genetic facts, which in themselves are assumed to be the products of selection of dominance modifiers. Further, the nature of the mutants and their consequent effects upon the phenotype must have been such as is required by the known interaction of two different dominants in producing only the three types of females in the different possible recombinations (see Table 3). Finally, in most cases, the mechanism of sex-controlled heredity was present from the beginning or established later, and *all* the selected groups of modifiers belonged to the group of sex-controlled mutants.

This is the type of evolution which is compared with the evolution of sex. The switch-gene is compared to the primary sex-genes. We could point out that the switch action of the primary sex determinants, whether one or many, is made possible by a unique chromosomal mechanism which controls a balance situation in two possible directions. No similar mechanism is known outside of sex-determination. But let us forget this difficulty and accept the rather superficial comparison of the two switch-processes as permissible. In the case of mimicry the "switch-gene" is a wing-pattern mutant towards the pattern of the model. The supposed modifiers and secondary mutants also

affect the pattern in the same direction, in presence of the "switch-gene." In sex, the "switch-gene" affects the development of the sex-cells and their surroundings (gonads, maybe ducts). A parallel to the mimicry case would require that modifiers and mutants are selected which act upon sex-cells and gonads. But what is meant in the comparison is a selection of somatic characters which have nothing to do with sex though they are brought under sex-control in some cases. Let us assume that horns in sheep or antlers in deer had been selected in the neo-Darwinian way. The same may be true for the differences in skeleton, muscles, brain, size, shape, etc., of the two sexes. This means, if it actually happened that way, that a series of simultaneous or consecutive changes were produced by selection of mutants and modifiers each of which improved upon some different system of the body, but none of them upon the pattern (sex) controlled by the "switch-gene." A parallelism between the two processes under comparison could be established only if, in the sphere of sex, selection during evolution produced different types of primary sexes, which is more or less absurd, at least in higher animals. Thus the comparison with evolution of secondary sex-characters is completely misleading and does not furnish a model for the supposed type of evolution of mimicry. Actually the only *tertium comparationis* is the fact of sex-control itself, which in general means the subjection of somatic characters to a switch-reaction with the products of the primary sex-determiners or of their secondary products, the sex hormones. But the problem of sex control is not at all under discussion, especially as sex-controlled inheritance is not necessarily connected with mimicry.

At this point it will be objected that mimicry actually affects many different characters, not only the pattern. In the Papilios the tails might be included and the type of flight, in others some other characters. This subject will be considered below. Here it suffices to say that the decisive part of the mimicry under consideration is the wing pattern. Otherwise one could not speak, as has been done, of tailed mimics when the model has no tails (see fig. 2d, e). Nobody who accepts Punnett's theory would deny the possibility of mutations in other organs and their selection, which might perfect still more the similarity already produced by the wing pattern. But the real problem remains the wing pattern which alone covers the major part, actually all or almost all, of the adaptation under discussion.

(*To be concluded*)

NEW BIOLOGICAL BOOKS

The aim of this department is to give the reader brief indications of the character, the content, and the value of new books in the various fields of Biology. In addition there will frequently appear one longer critical review of a book of special significance. Authors and publishers of biological books should bear in mind that THE QUARTERLY REVIEW OF BIOLOGY *can notice in this department only such books as come to the office of the editor. The absence of a book, therefore, from the following and subsequent lists only means that we have not received it. All material for notice in this department should be addressed to B. H. Willier, Editor of* THE QUARTERLY REVIEW OF BIOLOGY, *Department of Biology, Homewood Campus, The Johns Hopkins University, Baltimore 18, Maryland, U. S. A.*

DARWIN AND SOCIAL THEORY IN AMERICA

A review of *Social Darwinism in American Thought 1860–1915*, by Richard Hofstadter. *Philadelphia* (The American Historical Association; University of Pennsylvania Press); *London*, (Oxford University Press). $2.50. viii + 191 pp. 1944.

By Raymond P. Hawes, Goucher College.

In this engagingly written book Hofstadter is concerned with the coming of evolutionary ideas to America, the impact of these ideas on American thought and life and the reactions of outstanding Americans to them—including attempts on the part of American thinkers to reinterpret them or to replace them. The author's main interest is in the implications of biological concepts for ethics and social action.

Instrumental in introducing Darwin and Spencer to American readers were chiefly Asa Gray, E. L. Youmans, John Fiske and Chauncey Wright. William James started the stream-lining of psychology and philosophy along evolutionary lines, and William Graham Sumner did the same for the social sciences. In the sixties and early seventies, biologists—notably O. C. Marsh—contributed to the evidences of evolution. By 1873 it was possible for an editor to refer to the "'universal drenching' of belles lettres and journalism with natural selection." In the eighties "evolution" found its way into the churches, and opposition to it on the part of the outstanding Protestant theologians died out.

The ideas of Darwin and Spencer exerted a tremendous influence on American thought, and the uses to which these ideas were put were exceedingly varied. Many saw in them a support for a laissez faire economics and politics. Indeed, Spencer himself (followed in part by Sumner) outdid the originators of the laissez faire philosophy when he opposed state-financed education, health measures, and relief for the poor. The principle of natural selection was thought to imply that the unfit should perish and that among the unfit should be counted—along with the physically and mentally defective and those given to vice—the poor. Spencer was far from being alone in holding that it is a mistake to interfere with natural laws and with the natural, gradual growth of society, even by means of the mildest social legislation; while to attempt seriously to remodel the whole social system is "the greatest folly of which a man can be capable" (Sumner).

It was easy to reason that social evolution, like biological evolution, involves both a struggle of life against its non-living environment and a struggle of organism against organism and group against group. From this it seemed to follow that unrestricted economic competition is an essential of social progress; that those who scale the heights of power and wealth are necessarily the fittest; that these "superior" persons deserve whatever they can get and merit the utmost acclaim of their fellows; and that the losers should accept any hardship involved as a necessity imposed by nature. In short, the control of economic change by automatic adjustments in accordance with natural laws appeared to be the sole basis for freedom, justice, prosperity, and progress. To many it also seemed to follow that (despite Spencer's dream of the ultimate triumph of altruism and pacificism) war is an inescapable element of human life—quite clearly if society is founded on the man:land ratio. In the minds of a few, war took on the guise of a boon to mankind as an indispensable method of social evolution.

From these conclusions—perhaps in some cases with the help of Spencer's organismic conception of society and De Vries's mutation theory, which, as against Spencer's gradualism, seemed to legitimize sudden change—it was no great step to the acceptance of the validity of inferences such as the following. Economic misery and the irresponsibility of the rich are goods, not evils. The masses should follow "leaders" selected for them by "natural" processes. Brutal self-assertion and tyranny are justified. Imperialistic expansion (or conquest) is a nation's manifest destiny. Weaker (or backward) peoples and weaker (or "inferior")

races should be subjugated (or eliminated) by the stronger (or "superior"). The Aryan (or the Teuton or the Anglo-Saxon or the English-speaking people) is superior. Security lies in outstripping all other groups in military and industrial, if not also in population, "preparedness." The most important aspect of education is the cultivation of personal prowess and the martial virtues. Group suicide and group degeneracy are the greatest sins. Eugenics is the panacea.

In point of fact, those were not wanting who leaped to the most sweeping generalizations: that might always makes right; that human life as such merits no respect; that altruism, humanitarianism, and Christian ethics are bad, and that atheism is preferable to religion. According to Sumner, not only are there no natural rights, but also no ethical standards whatsoever—apart from "folkways."

Ideas such as the foregoing carried Social Darwinism a long way from Darwin, as Hofstadter clearly recognizes. While Darwin's *Origin of Species* was "Hobbesian in spirit," he finds, and while Darwin's remarks on "Natural Selection as Affecting Civilized Nations" in his *Descent of Man* were Spencerian and Malthusian in part, nevertheless, Darwin counseled against a ruthless elimination of the weak, however injurious to the race might be the perpetuation of our practice of caring for the weak and allowing them to propagate. Far from holding that might is right, Darwin discovered natural roots for sympathy and cooperation; asserted that man's moral sense is a critical factor in group survival; and thought of the "fittest" as those best adapted to existing conditions. The latter were not necessarily the strongest, far less the most brutal. As Nasmyth (following Kropotkin) discerned, in Darwin's view man owes his dominant position in the universe not so much to the struggle of individual against individual or to contentiousness, as to his struggle against his environment, along with unselfishness, mutual aid, and social coherence. Patten (followed by Cooley) called attention to Darwin's assumption that man is plastic or pliable with reference to his environment, so that circumstances may determine his characteristics. According to David Starr Jordan, Darwin believed that war is dysgenic. At the very inception of the evolutionary hypothesis in America, Asa Gray had tried to show that Darwin was "explicitly theistic"; while, at the turn of the century, Dewey suggested that if Darwin's "existing conditions" may be interpreted to include "the existing social structure with all the habits, demands and ideals which are found in it," we need not "go outside nature to find a warrant for the ethical process." Hofstadter might have pointed out that today outstanding biologists are developing this Darwinian interpretation of the application of biological ideas to ethics and social action rather than the "Social Darwinism" outlined above.

Hofstadter thinks that a new trend in American thought appears with the work of Lester Ward—a trend which was developed by a number of sociologists, economists, and philosophers, and one which in the end came to prevail over what had been known as Social Darwinism. Social evolution now comes to be considered a unique level of organization, with novelties "which are not predictable from a knowledge of their antecedents." On this social level of evolution we find new natural laws and a new principle of selection—variously called social, mental, purposive, artificial, and rational. Malthus's law has no validity for man, and the other laws which control the animal world apply to man in a very limited sense only. Not overpopulation and the niggardliness of nature, but the injustice of society becomes the villain in the piece, because with ever more rapid technological progress each new person can produce more than the last. Economics should be based on "abundance," not "want." On the social level at least, natural laws are not fixed and do not exclude reform. While the environment transforms the animal, man transforms the environment; control replaces mere adjustment.

Life on the animal level is no longer regarded—in Spencerian fashion—as a mere correspondence (or equilibrium) of two sets of relationships nor—in Darwinian fashion—as a mere struggle for existence. As William James put it, when consciousness appears upon the scene, the struggle is for "ends" (e.g., enjoyments); on the human level we are "fighters for the better." Neither animal struggle nor human competition selects the fittest in the sense of the best. A circle is involved in defining the fit as those that survive and then explaining their survival in terms of their "fitness." War and intraspecific competition are wasteful and injurious to the species and economic rivalry is self-defeating in that it generates competition-destroying monopolies. Natural laws no longer operate automatically to human advantage, and the favors of nature are not distributed according to merit. There is no biological or other "natural" basis for either laissez faire economics or for power politics.

In sharp contrast to natural selection, "rational selection" saves resources and produces superior beings. Man advances through the protection of the weak, through mutual aid and through responsible cooperation. From now on progress will come only by the exercise of free effort, through a deliberate selection between real possibilities, by intelligent planning on a social scale, and by using one part of the environment to reconstruct another. So far as government is democratic and aims at the good of all, the state should interfere with the automatic processes of nature. The functions of the state should be determined experimentally, but with the proviso that "human" values rather than impersonal values be kept in mind as the goal. In the words with which Hofstadter characterizes this new attitude: "Man's task is not to imitate the laws of nature, but to observe them, appropriate them, direct them."

This point of view pins its faith on non-eugenic means of progress, primarily: improving the environment, opening up opportunities and, above all, education. Ward, like Spencer—following Lamarck rather than Weismann—anticipated gains from "use-inheritance" in addition to the usual values of education. It also came to be widely believed that sociology should be based more on psychology than on biology, though Ward was quick to add that all sociologists should also be biologists. Pragmatists showed that the older psychologies (including Ward's own) were inappropriate as a basis for the social sciences, and promptly supplied a new psychology which was at once more "biological" and more "social" than the old. More specifically, mind must be considered: (1) a participant in progress, experimentally reconstructing both its environment and itself—not a mere spectator of inevitable change; (2) a "structure of propensities, interests and habits"—rather than a "mere machine for the reception and registration of pleasure and pain stimuli"; (3) largely a social product, and also socially oriented when operating on its highest (ethical) plane. For such a mind ideas become plans of action and instruments of control.

Hofstadter concludes that Darwinism "was a neutral instrument capable of supporting opposite ideologies." The earlier version of Social Darwinism was ruggedly individualistic because it came to birth in an age of unrestrained economic competition and unprincipled politics. In proportion as this "dream of personal conquest" met frustration, Darwinian collectivism of the nationalist and racist types pushed to the front and continued through an age of group assertiveness and competition down to the first World War, when Anglo-Saxon peoples "discovered" that Darwinian militarism was precisely what they were fighting. "As long as there is a strong element of predacity in society," Social Darwinism may rise again. At present, however, "most humanists," in attempting to understand society: (1) reject such ideas as "survival of the fittest"; (2) assume the uniqueness of the social level of evolution; (3) agree that progress rests on advances in technology and in social organization rather than on breeding and selective elimination; and (4) contend that naturalism as a philosophy does not preclude "moral sanctions which can be employed for the common good."

Hofstadter's book is well documented and his citations from source material are aptly chosen. It is possible that some readers would have welcomed a more extended discussion of the treatment of biological concepts by non-pragmatic writers. It must be admitted that it is hard to pick a quarrel with the author's conclusions. Very probably, most humanists among biologists—unlike those to whom Hofstadter alludes when he writes of "most humanists"—would not reject such ideas as "the survival of the fittest" in attempting to understand society. Doubtless one may be permitted to raise an eyebrow at an occasional assertion or implication, such as: (1) the statement that Herbert Spencer's philosophy is "a product of English industrialism"; (2) the attribution of some of Lester Ward's characteristic beliefs to his "humble origins"; or (3) the seeming implication (probably unintended) of certain passages in the author's "Conclusion" that the generally accepted economic (or political) system of an age determines how scientific discoveries are philosophically interpreted. But these matters are merely minor overtones in an excellent piece of work which constitutes a valuable supplement to the efforts of Beard, Gabriel, and Curti to interpret America's past.

REVIEWS AND BRIEF NOTICES

GENERAL BIOLOGY

THE BOOK OF NATURALISTS: *An Anthology of the Best Natural History.*

By William Beebe. Alfred A. Knopf, New York. $3.50. xiv + 499 pp.; 3 plates. 1944.

It took courage and must have given keen pleasure to collect in one volume "the best" from the great writings in the vast field of natural history. In his preface the author mentions "an invitation to every reader to damn my selection." Beebe's selection has evidently been influenced as much by the perfection of style and the inspired art of composition as by the scientific value and originality of the great contributions to natural history. Unquestionably he has succeeded in making a uniformly stimulating, charming, and thoroughly readable book.

With selections from the writings of forty-six authors, arranged chronologically, this anthology reflects the development of natural history from Aristotle to the present day. As a matter of fact, the author sees the inception of recorded natural history in the cave paintings from the stone age and opens the collected essays with three pictures of such admirable paintings by "An unknown Magdalenian (Circa 25,000–20,000 B.C.)." The first part of the book depicts the slow growth of man's understanding of animals and plants from early Greek times through the Middle Ages and beyond the Renaissance. It quotes from the writings of Pliny the Elder, Theobaldus, Gesner, Leeuwenhoek, Linnaeus, Humboldt, Thoreau, and others. The much larger, second part begins with Darwin and Wallace, includes Agassiz, Belt, Maeterlinck, Burroughs, and many more, and ranges to such contemporaries as Chapman, Julian Huxley, Seton, and Stefansson. The majority of the 31 selections for the second part have been chosen chiefly for their value as *literary natural his-*

tory and for having claim to consideration on the basis of "beauty of form or emotional effect."

Regarding subject matter, plants fare rather poorly, but animals are well represented by sample writings for nearly every interest from protozoa to mollusks, arthropods, and all the main groups of vertebrates. Besides which, there are essays on evolution, protective coloration, bird migration, the aims, adventures, and tribulations of naturalists, and other topics. Geographically the subjects range around the globe and from the Arctic to the Antarctic as well as from the Himalayas to under water. Eleven different nationalities are represented among the authors.

Unfortunately, modesty forbade the inclusion of selections from Beebe's own fascinating descriptions and interpretations of nature. However, the author's introductions to the two parts of his book make up in part for the deficiency, as they form interesting essays, equal in quality to the selected writings by others. Also noteworthy are Beebe's brief biographical notes concerning the authors selected for this anthology.

ADOLPH H. SCHULTZ

SIERRAN CABIN . . . FROM SKYSCRAPER. *A Tale of the Sierran Piedmont.*

By C. M. Goethe. The Keystone Press, Sacramento and San Francisco. $1.25. xiii + 185 pp. 1943.

This unusual book mingles natural history and plant ecology, Californian folklore, and propaganda for eugenics. Its style is highly individual, liberally besprinkled with capitals, literary and non-literary allusions, and odd bits of verse. The illustrations are abundant and excellent, but foreign words and scientific names are frequently mis-spelled.

It is difficult to determine whether the Main theme is that of the Mental and Spiritual REGENERATION of Skyscraper Man through the observation of Nature, or whether it is the DYSGENIC character of American Life and the Necessity for increasing the Reproductive rate of the Intelligent. Perhaps the balance favors the latter. The argument for positive Eugenics by controlling DIFFERENTIAL BIRTH-RATES is based on observations of Adaptation, Survival, and Extinction among members of the Californian Flora. But the author does not trouble to consider the difference between such interspecific comparisons and the intraspecific competition of human types, and blandly assumes that the genetic bases of mental differences and social behavior in man are comparable to those between Araucarian and yellow pines, for example. The importance of environmental factors in modifying mental differences and social behavior is simply ignored.

There is, nonetheless, much that is interesting for casual perusal between these covers.

BENTLEY GLASS

MAN DOES NOT STAND ALONE.

By A. Cressy Morrison. Fleming H. Revell Company, New York, London and Edinburgh. $1.25. 107 pp. 1944.

The title of this book was chosen as a challenge to Julian Huxley's concepts, recently developed in *Man Stands Alone.* Morrison, a chemist and former member of the National Research Council, approaches the problem of life from the standpoint of an avowed deist. He has undertaken to write a modern Bridgewater treatise, with arguments from the "fitness of the environment" and the marvels of adaptation. He accepts some sort of evolution, but has perhaps never heard of natural selection (at least it appears not to be mentioned anywhere). The following line of reasoning is fairly typical: "As the number of eyes in animals ranges from two to thousands, and all are different, Nature [sic] would have had a big job in developing the science of optics unless somewhere along the line there was a little help from Intelligence."

This edifice of biological logic is, however, completely vitiated by being based on the most astonishing statistical fallacy. The main thesis of the author, with which he begins and with which he closes his discussion, is simply that the existing universe could not have arisen by chance, because the mathematical probability of such an infinite number of coincidences is infinitesimal. He illustrates: the chance of picking at random a single white marble from a bag containing 100 marbles, the other 99 black, is 1/100; of doing it twice in succession in $1/100 \times 1/100$; etc., so that the probability of doing it five or more times in succession is altogether improbable.

Quite so! But let us suppose that each marble in the one hundred is identifiable, say by number. Then *any* sequence of five is equally improbable. Yet if you draw a sequence of five, regardless of what it is, you make an actuality of a coincidence that is highly improbable, as far as predictability is concerned. Every baby that is born represents a combination of paternal and maternal genes that is, from the standpoint of prediction, only one of trillions of possibilities. Yet babies somehow continue to be born! Of course, this, too, might be due to the machinations of Intelligence, the same Intelligence who determines how the penny will fall. Perhaps the author does not realize that he has reasoned himself into a position from which it follows that his God and Chance are one.

BENTLEY GLASS

THE NATURALIST'S LEXICON. *A List of Classical Greek and Latin Words Used or Suitable for Use in Biological Nomenclature, with Abridged English-Classical Supplement.*

By Robert S. Woods. Abbey Garden Press, Pasadena. $2.75. xviii + 282 pp. 1944.

The preface to this little lexicon opens with the claim: "Since Greek and Latin are seldom included in the studies of those who specialize in any branch of biology, scientific names are to most students of natural history simply meaningless and easily forgotten combinations of letters . . ." Even the many adequately educated biologists will welcome this convenient and well printed dictionary, regarding which the author states: "It is the purpose of this work to try to render more available to naturalists the definitions and correct pronunciations of these names which they so constantly encounter . . . . The intention has been to include not only classical words which have actually been employed in the construction of scientific names of animals and plants, but all others which might seem applicable to that purpose."

The "Classical-English" section contains 257 pages, listing alphabetically Greek and Latin words used in taxonomy and their equivalents in English. A philologist, rather than a biologist, may be able to explain the curious fact that words beginning with the letters *a*, *c*, *p*, and *s* seem to be far more common in taxonomy than words starting with other letters. At least this lexicon devotes a total of 125 pages to the four former letters (38 pages to the letter *c* alone), whereas only a total of 132 pages to all remaining letters. The "English-Classical" section of only 22 pages is too condensed to be of real service. For instance, only 66 names of mammals are listed and only 101 parts of the body, the latter under the inappropriate heading "Physiology."

This thin volume contains nothing that is not to be found also in the larger, general Greek and Latin dictionaries. To private libraries of biologists *The Naturalist's Lexicon* will form a handy addition.

ADOLPH H. SCHULTZ

EXPLORING BIOLOGY. *New Edition.*

By Ella Thea Smith. Harcourt, Brace and Company, New York. $2.24; tests, 36 cents. xxii + 619 pp. 1943.

EXPLORING BIOLOGY WORK BOOK.

By Ella Thea Smith and Lynda M. Weber. Harcourt, Brace and Company, New York. $1.00 (paper). vi + 154 pp.; tests, 16 pp. 1944.

The organization of this high school text is that known as the Unit-Problem. There are eight units, subdivided into thirty-one problems. Each unit deals with a basic understanding. These include the kinds of animals and plants and man's place among them, metabolism, health and disease, the interdependence of life, the bases of behavior, reproduction and development, heredity, and evolution. Each unit begins with a dramatic episode intended to serve as the first step in motivation. A number of these are exceedingly well written. Each of the problems is then introduced with a question, discussed accurately and with great clarity, involving a minimum use of technical terms, and concluded with directions for individual and group study in laboratory and in the out-of-doors, with a test of the factual information and the generalizations covered, thought problems, references, extra reading for ambitious students, and a list of the minimum number of new terms considered indispensable additions to the vocabulary. Each unit ends with a general summary.

The text is in two columns, a feature some will like and others dislike. The abundant half-tone illustrations are well chosen but have suffered from mediocre printing and paper. The diagrams are exceptionally good. There is a section of suggestions for the classroom library, a full and accurate glossary, and a very full index. An envelope containing a series of 29 tests of the objective type, prepared with great technical care, is also included.

The workbook to accompany the text has been prepared with the same thorough care and evident skill that went into the text. Seventy-seven exercises are included, and space for drawings, records, and answers to questions is provided. The sheets are punched and removable. There is a supplementary pamphlet of tests supplied to the teacher for each student.

There are too many excellent features of this textbook for individual consideration. After having examined and reviewed a considerable number of other high school texts, many of them good, the reviewer is more than ever impressed by the present one. In no other has he seen the standard of factual accuracy so high, the clarity of presentation so continuous, the provision of helps for teacher and students so abundant. Motivation and organization have been carefully thought out. The preview is one of the best introductions to biology to be found. The view of the entire subject is comprehensive and well balanced, plant, animal, and human biology being closely interknit. The style is appropriate for high school students.

No one but a high school teacher of a most exceptional character could have written this book. Other high school teachers should give it an enthusiastic reception.

BENTLEY GLASS

A FIELD COLLECTOR'S MANUAL IN NATURAL HISTORY. (*Publication 3766*).

Prepared by Members of the Staff of the Smithsonian Institution. The Smithsonian Institution, Washington. 50 cents (paper). iv + 118 pp. 1944.

In this pocket manual there are clear and concise directions for collecting, killing, preserving, packing and shipping most kinds of animals and plants. Prepared especially for men of the armed services abroad, it also contains some information on occurrence and dangerous forms. There is also a brief section on anthropological materials; a considerable one on fossils; and, finally,

one on other types of geological specimens. It is to be hoped that this handbook will serve as a stimulus to our men, who have so unparalleled an opportunity to enrich American museum collections. What they need to know, in so far as a manual can give it, is here. Experience will supply the rest.

BIBLIOGRAPHY OF REFERENCES TO THE LITERATURE ON THE MINOR ELEMENTS *and Their Relation to Plant and Animal Nutrition. Fifth Supplement to the Third Edition.*

Compiled by L. G. Willis. Chilean Nitrate Educational Bureau, Inc., New York. Paper. 96 pp. 1944.

This supplement abstracts additional literature on the role in nutrition of Al, Sb, As, Ba, B, Br, Cd, Ca, Cl, Cr, Co, Cu, F, Ga, Ge, I, Fe, Pb, Li, Mg, Mn, Hg, Mb, N, Pt, Ra, Rb, Se, Si, Ag, Na, Sr, S, Tl, Th, Sn, Ti, U, V, Zn, Zr, and the rare earths. There are four indexes, respectively of elements, of plants, of animals, and of authors. To all workers in the fields of nutrition this bulletin should be indispensable, and to many others it will be of great value.

ECOLOGY

TRANSACTIONS OF THE NINTH NORTH AMERICAN WILDLIFE CONFERENCE *April 24, 25 and 26, 1944, Chicago, Illinois.*

Edited by Ethel M. Quee. American Wildlife Institute, Washington. $1.00 (paper). iii + 376 pp. 1944.

A good idea of the progress and changing ideas in the field of wildlife management can be obtained by reading through these transactions. One is impressed by the number of articles concerned with controlling the larger game that have increased to or beyond the optimum carrying-capacities of the areas established for their propagation, especially the winter ranges. Such seems to be the case for mule deer in Utah and Oregon, and for elk in Jackson Hole.

Again, emphasis is placed not so much on the direct control of the stock as on the management of the habitat. In fact, wildlife management has so changed its methods in the past few years that many of the hunting and fishing laws are now antiquated, and reforms are needed. One startling idea proposed is the abandonment of all fresh-water fishing regulations,—this by Langlois, who believes that regulation of fishermen is negative, expensive and futile. Habitat improvement is a positive procedure and a justifiable way of spending the fishing-license funds. Another observation that may surprise some, though certainly not the ecologist, is the discovery by Cartwright that the Hungarian partridge and the sharp-tailed grouse have been saved from practical decimation by predators. The destruction of a substantial portion of first and second nestings by the predators was found to stagger the nesting attempts, thus becoming a major factor in the survival of the species during periods of inclement weather. This is certainly a far cry from the formerly all too common (and still very much in existence) policies of "shoot the vermin," often wantonly approved by conservationists themselves.

The deep sea fisheries are included for the first time in the conference program, and several articles discuss not only the problems and methods of marine fish management, but also some of the legal aspects of maritime fishing, with suggestions for post-war changes.

Two interesting reports discuss the effects of soil fertility and the relation of soil types to the abundance and quality of wildlife. Other papers deal with the role of government and private organizations in their efforts to cooperate with the Fish and Wildlife Service and state conservation agencies in protecting and managing the lands and waters for wildlife. Several speakers sharply attacked certain federal agencies for their utter disregard of wildlife; the justification for these castigations may be complete or partial, but at least their airing indicates that the program was well represented by all interests. The Transactions close with an important section devoted to the place of conservation in the educational programs of our schools and colleges.

HENRI SEIBERT

A PRELIMINARY STUDY OF THE THERMAL REQUIREMENTS OF DESERT REPTILES. *Bulletin of the American Museum of Natural History, Volume 83: Article 5.*

By Raymond Bridgman Cowles and Charles Mitchill Bogert. American Museum of Natural History, New York. (paper). Pp. 261–296; plates 19–29. 1944.

This paper presents the interesting results of a careful study of the thermal relations of desert lizards and snakes. The data are carefully selected for freedom from the influence of extraneous factors and consequently are not extensive. The conclusions will be of interest not only to ecologists but also to students of animal behavior and in particular of evolution. The mean temperatures of the normal activity range and the critical maxima are considerably lower than those reported in some earlier investigations, or than might have been expected in desert poikilotherms.

EVOLUTION

EVOLUTIONARY ETHICS. *The Romanes Lecture Delivered in the Sheldonian Theatre 11 June 1943.*

By Julian Huxley. Oxford University Press, London. 75 cents (paper). 84 pp. 1943.

A little over fifty years ago T. H. Huxley, valiant pioneer of the theory of evolution, gave the Romanes lecture on "Evolution and Ethics." In 1943 his grandson, Julian Huxley, one of the foremost modern students of evolution, delivered the Romanes lecture on the same subject. It is reprinted in this pamphlet. The approach of the two biologists to a relation between ethics and evolution is yet basically different. For the elder Huxley, values were founded on immutable, self-evident principles, and ethical progress consisted rather in "combating" the cosmic evolutionary process than in forming part of it. For Julian Huxley, there are no absolute values. He sees evolutionary processes not only on the inorganic and biological level, but equally on the sociological level. By thus extending the concept of evolution he finds an escape from ethical relativism. The trend of evolution yields criteria to judge moral values and discriminate between more advanced and more primitive forms.

Before discussing the contribution of the concept of evolution to ethics, the development of ethical behavior from early childhood to maturity is described, though in a rather superficial and dogmatic fashion. The deciding influence of the environment on the formation of the ethical values is stressed. Thus we find an enormous variety of ethical systems, but in the seeming chaos an evolutionary trend can be discovered. It is this trend which Huxley thinks will save us from ethical relativism and give us the right to decide that one system is more right than another.

What are these principles of evolutionary ethics? Characteristic of evolution are increase in complexity and degree of organization. In the ethical field this means that good is what helps the fullest development of the human individuality, the progressive realization of possibilities which have value for their own sake. Social organization is a means for the advance of the individual; it is good when it serves that development of individuals. Social change is to be encouraged because it leads to a realization of ever more possibilities in evolution. Yet this change can only be realistic and effective if it is based on knowledge: thus science receives increased moral value.

The main points which crystallize out of the discussion are: 1. There is a manifoldness of ethical values in various human groups. The ethical behavior of the individual develops under the formative influence of the specific cultural environment. 2. There is not only variation but evolution. We can apply the principles of evolution to the social level. As a matter of fact evolution is taking place at present at the fastest rate on the level of social, cultural organization. Ethical values are not equally right. The characteristic trends in the evolutionary process give us criteria to judge different ethical systems. But no new ethics is developed here. The content of this "Evolutionary Ethics" is not new. In fact, Huxley's ethics is essentially the ethics of the humanistic-Christian individualist, and it retains all the conflicts and contradictions which have led into the moral chaos of the present Western Civilization. We also find little new insight into the puzzles of ethical behavior or the characteristics of its development in the individual, or its evolution in society. Nevertheless, these lectures are of interest as an attempt to expand evolutionary concepts to a sociological field like ethics and as the expression of the point of view of an eminent modern biologist on one of the most important problems of our society.

HANS RIS

GENETICS AND CYTOLOGY

ELEMENTS OF BACTERIAL CYTOLOGY.

By Georges Knaysi. Comstock Publishing Company, Ithaca. $3.50. xii + 209 pp. 1944.

The purpose of this book is to give a brief and interpretative presentation of bacterial cytology. No attempt is made to include all of the important literature, since, according to the author, this would defeat the purpose of the book. However, much original literature on a variety of subjects is covered. The topics presented in the thirteen chapters include: Form and Size of the Bacterial Cell; The Cytoplasm and the Nucleus; The Cell Wall and the Slime Layer; Physico-Chemical Properties of the Bacterial Membranes; Cell Division; Vacuoles and Reserve Material; The Motion of Bacteria; The Spores of Bacteria; Staining; Bacterial Cultures; Cytology of the Actinomycetes; Cytology of the Spirochetes; and Cytology of the Myxobacteria. The book is well illustrated with 91 figures, 10 plates and 18 tables.

Because of the presentation of such a variety of topics in such brief form, most of the chapters serve only as outlines of the subject. The significance of a great deal of the material is inadequately discussed, and lack of additional data may, in many cases, leave the reader confused. For example: the author uses the term "bacterial nucleus" throughout the book but fails, in the chapter dealing with "The Cytoplasm and the Nucleus," to give the criteria or definitions which the cytologist uses for the bacterial nucleus. Some opinions to the contrary, the hypothesis that the bacteria have no nucleus does not deny the existence of a material capable of giving the usual staining reactions obtained with nuclei; nor does it deny the existence of a mechanism of inheritance. The continued use of the term "bacterial nucleus" throughout the book, is, therefore, misleading. In the chapter dealing with the "Physico-Chemical Properties of the Bacterial Membranes" one would like to know the evidence which leads the author to conclude that narcotics reduce the permeability of the cell membrane. In other forms, the few experiments which indicate a reduction in permeability of the cell membrane under narcosis are still open to question, while many experiments indicate an

increase in permeability under narcosis. The experiments dealing with the bacterial cell membrane are even more inconclusive. The effect of pH on the passage of solutes through the cell membrane is not considered, although one might well expect such in relation to morphological changes during growth. There are a number of topics that one would like to have seen discussed in a book of this type. To some it may seem unfortunate that a chapter is not devoted to a consideration of bacterial cytology and taxonomy. The book will be found useful, however, by students of bacteriology as a guide to the field of bacterial cytology.

W. D. McELROY

GENERAL AND SYSTEMATIC BOTANY

WILD FLOWERS IN BRITAIN.

By Geoffrey Grigson. William Collins of London; Hastings House, New York. 4s. 6d; $1.25. 48 pp.; 12 plates. 1944.

This very artistic and rather charming little book is written, interestingly enough, by a poet who has acquired an unusually thorough knowledge of the flowers which grow wild in the British Isles. In his account of the wild flowers, common and uncommon to the English landscape at various seasons, he has included many curious and interesting facts about their history, distribution, and adaptability. The text is well illustrated with twelve full-page color plates and twenty-two illustrations in black and white, many of them full-page. All are engravings reproduced from 18th and 19th century manuscripts. The book is not a key.

DEPENDENT PLANTS. *The Basic Science Education Series.*

By Bertha Morris Parker, with the collaboration of Ruth M. Addoms. Row, Peterson and Company, Evanston, Illinois. 32 cents; 24 cents in quantities of 5 or more. Paper. 36 pp. 1944.

This booklet introduces to readers of these columns a series of science books for children in grade school that, to judge from the present example, deserves the widest attention and use. The quality of the illustrations, most of them in color, is of such excellence both in drawing and in printing that adult scientists may want to add it to their personal libraries. The text, dealing with mushrooms, molds, slime molds, yeasts, bacteria and heterophytic seed plants, is scientifically accurate, on the one hand, and, on the other, is told in a manner to appeal to a child in the intermediate school grades. It is hard to imagine one whose interest would fail to be quickened by the story, or who would not be tempted to try at least some of the experiments and observational activities listed at the end under the heading, "See For Yourself."

TRAVELERS ALL, *The Story of How Plants Go Places.*

By Irma E. Webber. William R. Scott, Inc., New York. $1.25. 30 pp. 1944.

This book for young children tells in text and pictures of various ways by which plants achieve dispersal. The colored pictures will no doubt appeal to children, but they are crudely printed for a book so expensive. The text is well written, and children of eight to ten years to whom it was read gave every sign of interest and appreciation.

WILD FLOWERS AND WEEDS.

By G. H. Copley. John Crowther, London. 8s 6d. 164 pp. No date.

This book will be of interest to a strictly limited public —the English country walkers who have just begun to look at and enquire into the nature of the trees, herbs, and flowers which help to make up "scenery." It might appeal especially to children as an introduction to plant life and natural history, but the reviewer is a little doubtful as to whether its chatty style will be palatable to many adults, and in any case a real nature enthusiast will quickly graduate to more advanced reference books. The last part of the book, dealing with weeds and their control, is, however, of real practical importance, and the reader who starts out with sheer curiosity about wild flowers will at least end up with a gobbet of sound instruction on weeds. It is unfortunate that the reproductions of wild flower photographs are technically very poor. The price seems exorbitant for a book of such slight content judging by pre-war standards, but presumably that is because books have become a luxury product in wartime Britain.

EILEEN SUTTON GERSH

GENERAL AND SYSTEMATIC ZOOLOGY

ONE DAY ON BEETLE ROCK.

By Sally Carrighar. Alfred A. Knopf, New York. $2.75. 196 pp. 1944.

This is the tale of one day, the same day, in the lives of the animals of Beetle Rock—the weasel and her kits, the unmated injured Sierran grouse, the lively chickaree who had to get a nest built, the black bear and her two cubs, the lizard who nearly lost his life and found a mate, the coyote family from the plains which found the new life in the mountains difficult, the deer mouse, the Steller jay, and the mule deer who was growing too old to reign unchallenged as herd buck. The interplay of the lives of these inhabitants of the Rock is traced through thunder storm and through danger, in the early warmth of spring and the coolness of mountain air, from the stillness before the dawn to the darkness of a new night. Only a keen observer and a true lover

of mountains and forests and the living things that inhabit them could have written so unaffectedly of these simple doings. There is no false sentiment here, no anthropomorphism—it is sound natural history. Yet only an artist could have succeeded so well. The excellent wood-cuts are thoroughly in harmony with the spirit of the book.

BENTLEY GLASS

LABORATORY MANUAL FOR GENERAL ZOOLOGY. *By Tracy I. Storer. McGraw-Hill Book Company, Inc., New York and London.* $1.25. viii + 150 pp. 1944.

Storer's manual is designed to accompany his "General Zoology." In accordance with the plan of this text, the manual is divided into two parts. The first part deals with animal biology in general, while the second consists of exercises on individual invertebrate forms. Most of the first part is on the anatomy of the frog which is treated quite comprehensively. In addition, there are exercises on such subjects as digestion, nervous responses, mitosis, embryology, heredity, ecology, etc. On the whole, the treatment of vertebrate physiology is very brief and is the weakest part of the manual. It seems unfortunate that the instructor has not been given greater latitude by the inclusion of more exercises on this subject. The organization of the individual exercises is excellent, and the format is in keeping with the high standards of the McGraw-Hill Publications in Zoological Sciences. Nevertheless, the manual represents no radical departure from the usual zoological course with its major emphasis on anatomy, but with a little physiology thrown in as though it were an afterthought.

INSECTS IN KANSAS. *Common Insects of Kansas. Report of the Kansas State Board of Agriculture, June, 1943. Volume LXII, No. 255.*

By Roger C. Smith, E. G. Kelly, George A. Dean, H. R. Bryson, and R. L. Parker. Kansas State Board of Agriculture, Topeka. Free upon request (paper). 440 pp. 1943.

This manual is one which will be useful far beyond the borders of Kansas. It has been prepared for the general public, and particularly for farmers, county agents, biology teachers in the public schools, boys and girls, and similar groups. It contains a great deal of information on useful and injurious insects, beekeeping (Parker), life cycles (Dean), and methods of collection (Bryson). A forty-page list of injurious insects (Kelly), describing in tabular form the nature of the injuries inflicted by them, their life cycles, and methods of prevention and control, and giving references to the figures and descriptions of the main section of the manual, should be especially useful. The bulk of the manual consists of descriptions of between 800 and 900 of the commonest, most important, or most typical Kansas species (Smith). These are arranged by orders and families, following Essig, with good figures of the great majority, and references to the taxonomic literature. There are six color plates, respectively of grasshoppers, the chinch bug, moths and butterflies, beetles (2), and bees. There is a full glossary and an adequate index. Keys are not provided.

The state of Kansas is to be congratulated on providing free for its citizens and others interested such a practical manual of insects.

STUDIES IN NEOTROPICAL MALLOPHAGA (III) [*Tinamidae No. 2*]. *Proceedings of the United States National Museum, Volume 95. Number 3180.*

By M. A. Carriker, Jr. Smithsonian Institution, United States National Museum, Washington. Paper. Pp. 81–233. 1944.

This is the second report on the lice of the tinamous by Carriker. The group is one of "highly diversified and specialized genera," with the two main divisions of the host family parasitized by "strikingly different types." The monograph describes 2 new genera, 15 new species, 68 new subspecies.

THE CADDIS FLIES, OR TRICHOPTERA, OF ILLINOIS. *Bulletin of the Illinois Natural History Survey, Volume 23, Article 1.*

By Herbert H. Ross. State of Illinois, Department of Registration and Education, Natural History Survey Division, Urbana. $1.50 (paper). 326 pp. 1944.

Considering their close relationship to the Lepidoptera, the caddis-flies have in the past received surprisingly little attention. Betten's monograph on the Trichoptera of New York and the present one of Ross on those of Illinois elevate the group to its rightful place. This one, based on the collection of 750,000 specimens and the identification to species of no less than 150,000, raises the number of species recorded from Illinois from 37 to 183, and includes additional species from nearby regions which will probably be found in Illinois in the future. The immature stages of no less than 120 of these species are described. The biology and ecology of the group is discussed. Areas of distribution of representative species are mapped. Methods of collecting and preserving are described. The taxonomy is reviewed, and extensive revised keys to the families, genera, and species are given for adults, for pupae, and for larvae. There are concise descriptions and records of each species, with neotypes, holotypes, allotypes, and paratypes. The illustrations are outstanding, both the drawings of parts used in identification, for

their clarity, and those of the entire insects, larvae with or without cases as well as adults, for their delicate beauty. The illustrator, Dr. C. O. Mohr, deserves the highest commendation. The monograph ends with check list, bibliography, and index. It is unquestionably a most valuable contribution to insect taxonomy.

INSECTS OF PORTO RICO AND THE VIRGIN ISLANDS *Lepidoptera (Suborder) Rhopalocera, (Superfamily) Papilionoidea (True Butterflies), (Superfamily) Hesperioidea (Skippers). Scientific Survey of Porto Rico and the Virgin Islands, Volume XII, Part 4.*

By William Phillips Comstock. The New York Academy of Sciences, New York. $2.00 (paper). Pp. 421–622; 12 plates. 1944.

This survey of the butterflies of Porto Rico is based principally on the collections of the American Museum of Natural History and on two private collections. The arrangement follows that of the *Insecta Borinquensis*, by G. N. Wolcott. The check-list includes 110 species and subspecies, 97 of them personally confirmed. The bulk of the monograph consists of the descriptions of individual forms, including notes on the larvae, food plants, and occurrence. There is a key to the families represented. Numerous figures of venation are included, and many forms are illustrated in the rotogravure plates. The faunal distribution is discussed in a final section. There is an extensive bibliography but no index.

This monograph will be valuable not only to workers in the systematics of the Lepidoptera but also to students of zoogeography. It has every mark of a careful and thorough study.

THE FISHES OF THE FAMILY CHARACINDAE FROM VENEZUELA, WITH DESCRIPTIONS OF SEVENTEEN NEW FORMS. *Proceedings of the United States National Museum, Volume 95. Number 3181.*

By Leonard P. Schultz. Smithsonian Institution, United States National Museum, Washington. Paper. Pp. 235–367. 1944.

This monograph of Venezuelan freshwater fishes of the family Characinidae records 58 genera, and 117 species and subspecies, of which 3 genera and 17 species and sub-species are new. It is especially interesting that the forms of the Maracaibo Basin and of the Orinoco system are almost entirely different. Of 29 species from the Maracaibo Basin, for example, only 2 are known from the Orinoco system.

THEY HOP AND CRAWL.

By Percy A. Morris. The Jaques Cattell Press, Lancaster. $3.50. xii + 253 pp. 1944.

In this unusually attractive book the author has given his readers a most interesting account of the life habits of the reptiles and amphibians found within the borders of the United States, especially those forms occurring east of the Mississippi. His wide field experience as naturalist and collector has given Morris the great advantage of being able to record first-hand facts and information. Throughout the text he emphasizes the fact that the majority of this country's cold-blooded animals are not only harmless and inoffensive but actually beneficial.

Approximately one half of the book is concerned with snakes, both harmless and poisonous types. This is not an undue proportion of the space when one considers the fascination with which mankind has always regarded the serpent. In view of the enormous amount of misinformation about snakes, the author has very appropriately included a chapter entitled "Snake Fallacies," in which he explains most of the strange myths which have no foundation whatsoever, yet are sincerely believed by a great many sensible people.

The text is bountifully illustrated with more than a hundred fine photographs of the various animals described, all taken in their natural surroundings. While written in particular for the amateur, the many attractive features of this book will also appeal to the more professionally minded reader.

THE WAY BIRDS LIVE. *Second Edition.*

By Edward A. Armstrong. Lindsay Drummond Ltd., London. 7s. 6d. 96 pp.; 16 plates. 1944.

Intended primarily for children, this little book will prove worth-while reading for any amateur ornithologist. The manner of mate attraction and selection, the various types of adornment and their use in display, courtship gifts and feedings, and other kinds of behavior prior to egg laying are briefly described. The story continues by telling of the eggs, the young, their hatching, and their powers of learning versus their inborn knowledge. Communal behavior, roosting, food, migration, and pointers on methods of bird watching complete the book. Photographs and sketches by the writer illustrate the various activities of the birds. Although the discussions are very short, they provide a preliminary background to certain aspects of bird life usually missing in most handbooks.

HENRI SEIBERT

SOMERSET BIRDS AND SOME OTHER FOLK.

By E. W. Hendy with an introduction by H. J. Massingham. Eyre and Spottiswoode, London. 12s. 6d. 165 pp.; 15 plates. 1944.

Without doubt, this book is well written and some of the vivid descriptions of moor and marsh are expertly

rendered. The subject, as stated in the foreword, "... tells of my experiences with the birds of Exmoor and the Somerset countryside but also has something to say about other country creatures, human and unhuman."

Ornithologically, it leaves much to be desired, for the writer has sacrificed valuable data for the sake of fluidity of prose. Be that as it may, the chapters on the chaffinch, the merlin, the robin, and other denizens in and around Porlock contain informative material, much of it obtained by banding. Emphasis is repeatedly placed on observations in the field as the only way to learn about birds, yet apparently Hendy has the feeling that this is a method scorned by ornithologists. "Modern ornithology appears more and more to aim at reducing fieldwork to an elaborate system of census making and card indexing by teams of workers." (p. 63). There is a similar statement on p. 108. Further criticism is leveled at modern ornithologists, "against the 'intensive and American' methods of some modern ornithologists," because "these 'highly specialised programmes' tend to convert what is really a sport or recreation into 'a ruthless business proposition'." Nor does the author have a high regard for the professionals for refusing to accept certain sight records of rare birds.

The ancient controversy as to whether the female adder swallows her young is reopened, and whereas the writer does not commit himself one way or the other, he finds it difficult to believe that all eye-witness accounts are illusions, and so prefers to keep an open mind.

The photographs are excellent.

HENRI SEIBERT

THE BIRDS OF TIMOR AND SUMBA. *Bulletin of the American Museum of Natural History, Volume 83: Article 2.*

By Ernst Mayr. American Museum of Natural History, New York. 65 cents (paper). Pp. 123–194. 1944.

This check list is based on the collections made on Timor and Sumba by Georg Stein, with additional species collected by others included in the list to complete the compilation. Taxonomic notes on the birds of both islands follow the annotations. This section provides critical reviews of genera and of certain groups whose exact relationships have long been taxonomic puzzles. Many new subspecies are described.

The remainder of the report is devoted to the zoogeography of the two islands. On the basis of the composition of its avifauna, Timor is found to belong more closely to the Oriental than to the Australo-Papuan region. Ornithologically it is most nearly related to Wetar, although separated from that island by a deep channel. The land bridges claimed by Rensch to have existed between Timor and Sumba, Timor and Wetar, Timor and Celebes, etc., are disproved on the basis of the avian distribution. Mayr furthermore concludes with Wallace that Timor and Australia were never connected by land, although separated at one time by a strait of only 20 to 40 miles in width. The dispersal faculties of birds are thus emphasized, and distribution is made to fit more closely with geological evidence. The birds of Sumba are most similar to those of Flores and are considered as being derived from the Lombok-Alor chain.

HENRI SEIBERT

THE WOLVES OF MOUNT MCKINLEY. *Fauna of the National Parks of the United States—Fauna Series No. 5.*

By Adolph Murie. United States Department of the Interior, National Park Service; U. S. Government Printing Office, Washington. 40 cents (paper). xx + 238 pp. 1944.

This is an exemplary report on an extensive field study of the life histories and ecological conditions of the larger animals in the Mount McKinley National Park. Special attention is paid to the timber wolf (*Canis lupus pambasileus*) and the Dall sheep (*Ovis dalli dalli*), inhabiting the slopes of the highest mountain in North America, since the author had originally been requested to investigate the relationships between these two animals to determine the influence of the wolf predators on the number of sheep. It is very gratifying that the book has been expanded to include also accounts of the caribou, moose, grizzly bear, fox, and eagle in the same park area. The entire complex problem of the factors underlying the density of a wild animal population and the ceaseless struggle for survival has been considered in a thorough and informative manner, using wolf and sheep as special examples. Careful records on feeding and breeding habits, on the effect of climatic changes, on the prevalence of disease and its correlation with the age of the animals, etc., are enlivened by relevant accounts of specific incidents observed in the field.

Wolves prey chiefly on caribou, to a lesser extent on sheep and least of all on moose. Of sheep, only the young in their first year and old or diseased animals are killed. The golden eagle attacks young sheep very rarely, and the grizzly feeds on the ungulates mostly in form of carrion only. It is concluded that in this park area a normal prey-predator adjustment has been attained.

The report is illustrated with 58 excellent photographs and drawings, which alone are well worth the remarkably modest price of this splendid publication.

ADOLPH H. SCHULTZ

THE NATURAL HISTORY AND BEHAVIOR OF THE WESTERN CHIPMUNK AND THE MANTLED GROUND SQUIRREL. *By Kenneth Gordon. Oregon State College Press Corvallis.* 75 cents (paper). 104 pp. 1943.

This monograph, illustrated with attractive sketches by the author, considers in as complete a fashion as possible the biology of *Eutamias* and *Citellus lateralis*. The author has studied these little rodents extensively and over a period of years. He includes sections on taxonomy, description, distribution, biology (movements, dens, food, water, reproduction), ecology (environmental factors and reactions, community organization, population, economic relations), and behavior (sensory, reactive, and modifiable). Like the observations of social dominance, the experiments with mazes, problem boxes, and strings on aspects of learning, retention, and individuality are most interesting because, although not sufficiently extensive, they were conducted in the field on wild, and not on captive, animals. Gordon concludes by pointing out the numerous questions still to be answered regarding these relatively much observed and familiar mammals.

RAYMOND L. DITMARS. *His Exciting Career with Reptiles, Animals and Insects.* *By L. N. Wood. Julian Messner, Inc., New York.* $2.50. 8¾ x 6. x + 272. 1944.

This volume is another of the Julian Messner shelf of modern narrative biographies created to satisfy a desire among librarians, parents, teachers, and intelligent readers for really authoritative biographies of characters of interest for this generation. While the present recreation of the life of Raymond Ditmars is an award book of the Julia Ellsworth Ford Foundation for children's literature, adults as well as younger readers will find it unusually entertaining reading. As one reviewer has already commented, it does for the reader what Ditmars himself did for the public—makes snakes popular and understood as interesting creatures.

Raymond Ditmars was indeed a confirmed nature-lover. Early in life, we are told, he exhibited interest in all sorts of living things, particularly snakes, to such an unusual degree that even his own family regarded him as somewhat of a problem. When, at the age of seventeen, Dr. Beutenmuller of the American Museum of Natural History offered him a job as assistant, young Raymond was almost too overcome to answer. To his dismay, his parents were cool to the idea. Mounting butterflies at the museum might be pleasant work for a couple of months in the summer, but what prospect did it offer for a career. No one had ever made a success of life just by chasing butterflies and snakes!

From his associations at the Museum with such outstanding men as Chapman, Osborn, Gratacap, Beutenmuller and others, Ditmars learned a great deal besides responsibility and system. The encouragement and friendship which they gave him really launched him into his career as a scientist.

In the year 1899, at the age of 23, the one perfect job in the world for him came when he was asked to become curator of reptiles at the New York Zoological Park. Preparations were being made for the opening of the Park on the 261 acres of wilderness at the southern end of Bronx Park. Although the Reptile House was not yet completed, Ditmars, as soon as he joined the staff of the zoo, set to work to form a collection, with his own private collection of forty-five snakes representing fifteen species as a nucleus. Up until this time his very valuable collection had been housed on the top floor of the parental brownstone mansion in the Bronx. The young curator's primary concern in his new job was to expand the collection. He succeeded in this so well that by the first year he had acquired more than 400 reptiles. Under his expert management the reptile house became so entirely satisfactory to the public and to the directors that he was soon asked to take over the mammals as well. His relentless search for new and rare specimens took him to the far corners of the earth. The present volume records many extremely interesting and amusing incidents which occurred during these numerous and varied expeditions.

There can be no doubt that Ditmars had a happy flair for popular education. His numerous books were designed both to amuse and inform. Throughout his life he waged a campaign to arouse popular sympathy towards all forms of animal life, including those usually regarded as "repulsive."

That he succeeded very well in changing the attitude of the public is indicated by an editorial in one of the leading metropolitan newspapers in the spring of 1937, just 30 years after the publication of *The Reptile Book*, which hailed the beginning of the snake-hunting season with the statement "... snake hunts are growing positively popular...." Uncritical shudders at reptiles were giving place to intelligent interest in them. The day of the editor, once known to Ditmars, who had rejected the manuscript of a story about a snake by throwing it on the floor and jumping on it, was past.

MARY E. RAWLES

ANIMAL EMBRYOLOGY

OURSELVES UNBORN: *An Embryologist's Essay On Man. The Terry Lectures.* *By George W. Corner. Yale University Press, New Haven.* $3.00. xiv + 188 pp.; 8 plates. 1944.

Corner has chosen, in the Terry Foundation Lectures "on Religion in the Light of Science and Philosophy," to apotheosize the human embryo in a triptych, the panels of which portray respectively (1) the essential morphological and physiological aspects of normal human development, (2) the nature of the misfortunes

which can befall the human embryo during its development, and (3) the relationship of man to the other brutes as elucidated by the known facts of human development and placentation.

In his first essay, Corner has professed to cover the early developmental history of the human embryo as "an archive in which is written the evidence of its descent as an animal, a vertebrate, an amniote, a mammal, a primate." He has included in his review a brief schematization of the conventionalized pattern to which mammalian development can be reduced; a description, surprisingly but agreeably detailed for a popular treatise, of the method of separation of the so-called germ-layers and auxiliary membranes in the primate embryo; and an analysis of the relationship of the embryo to its uterine environment. In the second essay, the author has described and treated of various abnormalities of human development, ranging from local deformities through faulty implantation to erythroblastosis fetalis. In his final essay he has discussed first the historical development of the concept of evolution, next the modern anatomical and paleontological foundations for the classification of mammals and primates, and finally the light which embryology sheds on the position of man among his fellow-creatures.

Especially commendable is his success in relating the facts of embryology to those of evolution. His emphasis on the qualities of the primates as a generalized rather than a specialized group is particularly welcome in a book designed for popular consumption, as is his interpretation of the biogenetic law. "To say that the pharyngeal bars suggest a common origin for fish and man," states Corner on page 67, "is a very different thing from claiming that as embryos we humans have gills and therefore we must have had a fish for a direct ancestor." A very different thing it is indeed, but all too many workers even in this age drift into the more careless Haeckelian habit of thought or expression, and unfortunately in material presented to the serious student as well as to the general reader. Popularization of the sounder and more critical evaluation cannot fail to be salutary in a book destined for as wide dissemination as the present one.

The volume suffers to a certain extent from a lack of homogeneity in form. The author's exposition throughout is simple, straightforward, and admittedly everywhere lucid. But if at best his style aspires to the sonorousness of the rolling phrases of the Prophets, at its poorest it becomes vitiated by utterances more properly befitting the Philistines. One could wish that the author had indulged in more careful editing, for the purpose of attaining a higher degree of uniformity of expression.

The volume exhibits also some unevenness in content. The present reviewer wonders, for instance, whether the necessarily somewhat technical discussion of the immunological basis of erythroblastosis fetalis can be appreciated by the same reader for whom Corner has labored at length to lay the spectre of prenatal influence. The question arises, indeed, as to how easily many of the included materials, even with the benefit of Corner's excellent clarification of details, are assimilable by an audience unfamiliar alike with the facts, the methods, and the terminology of biological science. For the student already conversant with these materials, however, the volume provides an admirable summary of the data at hand.

JANE OPPENHEIMER

A LABORATORY MANUAL OF VERTEBRATE EMBRYOLOGY. *Revised.*

By Roberts Rugh. Burgess Publishing Company, Minneapolis. $2.00 (paper). x + 194 pp. 1944.

This manual sets a new high standard in the extent and completeness of material covered, in number and general excellence of illustrations, and in fullness of text. Indeed, by a process analogous to the one that has made destroyers in this war the size of cruisers in the last, and cruisers the size of battleships, this is a laboratory manual that has become a textbook, as was intended, largely on the descriptive level.

The bulk of the material, quite rightly, concerns the frog, chick, and pig, but there are sections on the general aspects of gametogenesis, fertilization, and cleavage. Conklin's figures of the development of *Amphioxus* have been reproduced from the *Journal of Morphology*. Directions, drawings, and photographs for the study of the early development of *Oryzias*, the Medaka fish, should prove extremely valuable as this practical, laboratory-breeding teleost comes into general use. Each section is followed by a dozen or so review questions and page assignments in standard texts. There are numerous blank spaces for student's drawings and numerous drawings for labelling. Give the students their slides and this manual, and the laboratory will largely run itself.

The chief general criticism—entirely a matter of policy—is that the manual deals almost exclusively with prepared slides. The embryologist who believes it important for students to roll up their sleeves and work with fresh material, to dissect amphibian blastulas under a binocular microscope, to remove from the egg and prepare their own whole mounts of chick embryos, or otherwise to manipulate embryological material will have to supplement. The manual is so arranged that this can be done.

Several minor faults can easily be remedied in subsequent issues. The section on meiosis is outdated and should be rewritten. The 43 photographs of frog development, admirable as they are, still do not show all the structures mentioned in the legends and could be sharper. When such a series of photographs is presented, would not the permanent usefulness of any manual be greatly enhanced if they tallied with stand-

ard stages of development—in this case with the stages given for *Rana pipiens* by Shumway? The term blastopore is introduced almost casually while some lesser terms are fully explained. Various figures from Patten are reproduced effectively and with full acknowledgment. At least half a dozen others that have been redrawn with only the most trivial changes should also have been accompanied by acknowledgments. These are, however, minor faults in an outstanding, competent piece of work.

G. B. MOMENT

ANIMAL MORPHOLOGY

A TEXTBOOK OF HISTOLOGY. *Functional Significance of Cells and Intercellular Substances. Third Edition.* *By E. V. Cowdry. Lea & Febiger, Philadelphia.* $7.00. 426 pp. 1944.

This new edition is not, as are so many revisions of successful texts, an expansion of the original. The effort has been made, and very successfully, to reduce the detailed treatment, to give a stronger emphasis to fundamentals, to focus "attention on the correlation of form and function." As in the earlier editions, the presentation centers around the blood vascular system and the fluid environment of the cells as the principal integrator, and a dynamic view of cellular integration and activity results. Still less than before is this text to be compared with such texts as Maximow and Bloom's. Those who want an exhaustively illustrated book that can be used as a reference in later work will still prefer the latter type. Those who are interested in cell differentiation and embryological histology will also have to look elsewhere. But those who want a simple and dynamic picture of correlated form and function, with half as many figures and far fewer in color, will prefer Cowdry's book. (One should note that the reduction in illustration is not accompanied by a lower price). For the elementary student of the subject, this should be an excellent guide.

ANIMAL PHYSIOLOGY

FUNDAMENTALS OF PHYSIOLOGY. *The Human Body: Its Functions and Structure.*

By Elbert Tokay. The New Home Library, The Blakiston Company, Philadelphia. 69 cents. xiv + 336 pp. 1944.

This volume is advertised as "a book which explains clearly the important things you need to know about the structure and function of the human body." The author has succeeded in giving a clear and simple description of the structures of the body and their function. The properties of living matter and the organization of the body are described in introductory chapters. These are followed by discussions of the circulatory, respiratory, digestive, excretory, endocrine, neuro-muscular, and reproductive systems. The final chapters of the book are devoted to a consideration of nutrition, metabolism, exercise, protection against disease, and the health of the body. Thus, many aspects of physiology have been touched upon, but one cannot say that this review contains all the facts one needs to know. There are a few bad mistakes, such as a faulty description of the mechanism of function of the carotid sinus, but on the whole the volume is a very creditable contribution to a set of books which is being published for the layman. The book, however, does not deserve the serious attention of students of medicine or advanced students of the biological sciences. They require a somewhat closer approach to the true and complex picture of physiological functions than the publishers and the author of this book seem to feel is desired by laymen. Many of the 150 illustrations specially prepared are adequate, but quite a few contribute little, and some are incorrect. For example, the diagram of the cerebellum on page 190 is oversimplified and labeled incorrectly; figure 108 is unnecessarily poor; figure 112 omits certain functionally important peculiarities of the thoraco-lumbar division of the autonomic system. The chief feature which recommends this book is its clarity, and those whose requirements are not great may find it to be completely satisfactory.

CHANDLER MCC. BROOKS

CHEMICAL ANATOMY, PHYSIOLOGY AND PATHOLOGY OF EXTRACELLULAR FLUID. *A Lecture Syllabus. Fourth Edition.*

By James L. Gamble. Department of Pediatrics, The Harvard Medical School, Cambridge. 75 cents (paper). 46 charts with text. 1942.

This is a reprinting of the fourth edition of a lecture syllabus which has become a standard work in physiology. It consists of a series of 47 charts and accompanying descriptions dealing with the volume, composition, and changes which may occur in the plasma and interstitial fluid constituting the aqueous environment of body cells. The various topics treated are: the role of extracellular fluid in regulatory reactions, the participation of the fluid in osmotic adjustments, the renal defense of the chemical structure of body fluids, the regulation of extracellular fluid volume, the pathogenesis of dehydration, acidosis and alkalosis, and the rationale of replacement therapy. This concise, yet thorough, discussion of the stability of the internal environment of the body cells is highly recommended to those physiologists and physiological chemists who are not already familiar with this work.

CHANDLER MCC. BROOKS

FEMALE ENDOCRINOLOGY *Including Sections on the Male. By Jacob Hoffman. W. B. Saunders Company, Philadelphia; London.* $10.00. xv + 788 pp. 1944.

This volume is a careful and thorough handbook, setting forth the pathology, diagnosis, and treatment of endocrine disturbances of the reproductive system and of related diseases. Its teaching is based on a full review of current knowledge about the physiology of reproduction in mammals. The text is clear and well arranged. Full, up-to-date reference lists are provided. The book will be useful to teachers of physiology as well as to clinicians and medical students. Its readers may find themselves at times wishing for more of the savor of personal experience. Hoffman, who in fact has had considerable experience as experimentalist, pathologist, and practitioner, reviews his topics with such painstaking care that his own judgments and conjectures do not always come to the surface. Soundness on a subject like this, however, may be at the present time preferable to individuality.

GEORGE W. CORNER

NEUROLOGY OF THE EYE, EAR, NOSE, AND THROAT. *By E. A. Spiegel and I. Sommer. Grune and Stratton, New York.* $7.50. xi + 667 pp. 1944.

This volume is intended as a survey of the present state of knowledge in the "borderland" between neurology and otolaryngology and ophthalmology. It succeeds in being an excellent approach toward a greater synthesis in the teaching of these fields of medicine. Aberrations of the special sensory and motor functions associated with the apertures of the head cannot be understood without a background of cerebral anatomy and physiology, just as these subjects are intelligible only when considered in relation to peripheral functions. The authors present a unified account of the functions and dysfunctions of the eye, ear, nose, and throat, and their associated cranial nerves and cerebral structures. Discussions include highlights of modern investigative results, and are obviously tempered by long experience in research, teaching, and clinical practice. As an attempt to cover the fields of anatomical and physiological fundamentals, pathophysiology, modern experimental research, clinical practice, and therapy, the text of six hundred odd pages is often synoptic. It is debatable whether or not the theme of unity is weakened by setting apart two final chapters as a brief review of the symptomatology of brain stem and cortex. The reviewer, for example, would have preferred where possible a complete integration of this material with the rest of the book. In view of the excellence of many of the illustrations, the crude execution of others, especially some of the line diagrams, is surprising. An extensive bibliography is appended. The book should be of interest and value to practitioners and advanced students in the specialties of ophthalmology, otolaryngology, and neurology.

DAVID BODIAN

HEALTH AND DISEASE

FOUNDATIONS FOR LIVING. *By Fern Silver and Mildred Graves Ryan. D. Appleton-Century Company, New York.* $2.12. x + 615 pp. 1943.

Although the aim of modern education has been carefully defined in terms of preparation for worth-while living, very few text books have been published with that aim as clearly in view as the present one. The volume is designed for use as a senior high school text in home economics courses, but it covers such a wide variety of topics in addition to the time honored principles of cooking and sewing, that it is truly a guide to at least one fundamental element of worth-while living: namely, intelligent, economic, and enjoyable homemaking.

The authors have broken through the stiff crust of accepted pedagogy, and have discussed, in the very first section of the book, such modern, yet practical, topics as boy and girl relationships, sex, courtship, marriage, good manners, and finding a job, all under the general heading if personal and social relationships. This section is not just a conglomerate mixture of Dorothy Dix and Emily Post, but rather a guide for intelligent young people in solving some of their most vital personal problems *now*, by some method other than that of trial and error.

In the next four sections, attention is directed to such practical yet fundamental factors in living as foods, clothing, personal appearance, and home management. No effort has been spared here in presenting sound, common-sense facts in a completely authentic, yet thoroughly understandable manner. Two particularly helpful sections covering consumer buying and home furnishing and care have been included. Under consumer buying the authors have presented a wealth of material dealing with the selection and purchase of a variety of products ranging from meats, canned goods, eggs and milk, to clothes and shoes. The final section on child care and guidance rounds out a well balanced and carefully prepared course of study that should contribute in no small manner to the successful home-making endeavors of its users.

The many graphic and photographic illustrations, as well as the chapter references and complete index, enhance the value of the text for either class-room or home use.

B. AUBREY SCHNEIDER

TO LIVE IN HEALTH.

By R. Will Burnett. Duell, Sloan and Pearce, New York. $2.75. vii + 332 pp. 1944.

The underlying principle and constant theme of this excellent work is the expression of a deep conviction that the practice of sound health habits can come only as a result of sound knowledge of scientific health facts. It has been the author's purpose to make available to the lay reader, in clear, non-technical language, a body of scientifically accurate facts concerning both personal and public health as related to the welfare of the nation.

Since the human body is the central figure in any consideration of personal or public health, much of the volume has been devoted to discussions of the common causes of death and disability in the American population, the performances of the body in warding off its common health enemies, and the physiological reactions of the human system in recovering from the ravages of disease and injury.

Wherever the opportunity presents itself, the author has used scientific facts to dispel common superstitions and false conceptions concerning the principles and practice of healthful living habits. The outstanding advances in our knowledge of bacteriology, immunology, parasitology, and nutrition over the past one hundred years have been presented in a popular, yet completely authentic manner.

The careful selection and logical presentation of the material will make the volume serve well for use in senior high school or college courses in health and hygiene, as well as in the home library. Many graphic and photographic illustrations are used in clarifying the general health problem of the nation.

An index and a list of preferred references relating to each chapter are appended.

B. AUBREY SCHNEIDER

AN INTRODUCTION TO PUBLIC HEALTH. *Second Edition.*

By Harry S. Mustard. The Macmillan Company, New York. $3.25. ix + 283 pp. 1944.

The materials and methods associated with the general field of public health have been clearly outlined in this superb text, which is designed especially for use in medical schools, nursing schools, general college courses in hygiene, and as an introductory course for regular students of public health. As in the previous edition, the discussions are largely devoted to the definition of public health terms and problems, and analyses of the purposes and methods of protecting the health and caring for the illnesses of the general population.

The chapters on communicable diseases have been revised to include the latest knowledge in the fields of bacteriology, immunology, viruses, and chemotherapy. The sudden impact of war-time living and working has introduced many new problems in the general public health picture in the United States; hence the present edition has incorporated new chapters on industrial hygiene and medical care.

Some readers may be irritated by the numbered-item, outline method of presentation; however, the overworked student will find this method very convenient for purposes of review or reference. Although the text is completely devoid of charts, graphs, or diagrams, and the tabular material is very meager, the work is thoroughly documented, and each chapter is concluded with a select list of references. An index is provided.

B. AUBREY SCHNEIDER

ESSAYS IN THE HISTORY OF MEDICINE *Presented to Professor Arturo Castiglioni on the Occasion of his Seventieth Birthday, April 10, 1944. Supplements to the Bulletin of the History of Medicine Number 3.*

Edited by Henry E. Sigerist and Genevieve Miller. The Johns Hopkins Press, Baltimore. $3.50 (paper). vi + 358 pp. 1944.

Generally there is not much ado over the anniversaries of the aging refugee scholar, cut off from his pupils and friends. Arturo Castiglioni, former professor of the history of medicine at Padua, and now connected with Yale University, has happily escaped this fate. On the occasion of his seventieth birthday he has been presented with this quite substantial volume, containing not less than 26 contributions in 6 different languages. This "Festschrift" bears witness to the general esteem in which Castiglioni, the man and the scholar, the author of a widely read and translated one-volume history of medicine, and of numerous studies covering especially the Renaissance period and magic in medicine, is held even outside of his unfortunate country.

None of the contributions of this volume deals with magic, while three papers concerned with Renaissance personalities and problems are among the tastiest slices of Castiglioni's birthday cake (J. F. Fulton, "Polydore Vergil"; C. F. Mayer, "Mignotydea"; C. Proskauer, "Der Zahnbrecher des Hans Sachs"). Iago Galdston and G. Sarton contribute two very attractive sketches of eighteenth century scientists, Ozanam and Beccaria. E. B. Krumbhaar-W. B. McDaniel's "Angina inflammatoria as described in David Orme's Edinburgh Dissertation (1749) and Benjamin Morris' Leyden Dissertation (1750)" and A. Magnus-Levy's "Diabetikerdiäten der Vorinsulinära" deal very competently with special chapters in the history of the actual practice of medicine. It is the reviewer's opinion that the future of the history of medicine as a living science depends directly on an increase of this type of study, which at present unfortunately is the Cinderella of medical historiography. G. Urdang's "Retail Pharmacy as the Nucleus of Pharmaceutical Industry" will be studied with great profit.

Particularly numerous throughout the volume are the contributions from Latin America. Most enjoyable is C. E. Paz Soldan's "Medidas de Seguridad contra la Fiebre Amarilla durante el Virreynato del Peru." North Americans will be glad to have J. B. Lastres' stimulating essay on "Medicina Aborigen Peruana," published a few years ago in Peru, now easily accessible in a North American publication. Carlos Martinez Duran, well known for his work on the history of hospitals in Latin America, gives an interesting survey on "Los Hospitales de América durante la Epoca Colonial." Nevertheless, the reviewer feels that Duran's evaluation of the Spanish Conquest in general as an essentially spiritual phenomenon and his unrestrained praise of a type of hospital more often created as a soul-trap for dying heathen than as a medical institution, is at least open to discussion.

Leonardo Olschki's "Medical Matters in Marco Polo's Description of the World" is perhaps the most fascinating piece among so many other interesting papers.

The reviewer, being unable even to enumerate more than a minority among the 26 contributions, is painfully aware of the arbitrariness of his procedure. He is certain that competent readers will find among the essays unmentioned not only several they will judge equal, but may even prefer to those discussed.

ERWIN H. ACKERKNECHT

THE ART OF THE HEALER.

By Bernard Aschner. Translated by Ruth and Heinz Norden. The Dial Press, New York. $2.75. viii + 306 pp. 1942.

Bernard Aschner began his career as a brilliant experimentalist. He was the first to remove the entire pituitary gland from a dog, and thereby to demonstrate the control of the gland over normal growth. He also showed that it was related to carbohydrate metabolism. And he discovered the oculo-cardiac reflex. In Europe he was well-known as a gynecologist and student of medical history. He is therefore entitled to respectful attention when he writes on healing.

His main thesis is provocative, and, to a degree, it is sound enough. Medicine, he thinks, has been so dazzled by the modern achievements of experimental science that it has unduly neglected the time-tested values of the medical knowledge of earlier times, and of the common folk. Here readers are in for their first shock. It is not the rise of bacteriology and the germ theory of disease that Aschner has in mind—these are scarcely mentioned in the entire book. The real villains of the piece are Bichat and von Virchow, who were responsible for the emphasis upon cellular pathology and diagnosis. Back to the Golden Age of medicine!—to the days when doctors like Boerhaave, Sydenham, and Hufeland followed Plato's dictum that "Good physicians apply their treatment to the whole body and attempt to heal the sick part or organ by treating the whole individual." This is Aschner's Constitutional Therapy. Early in his career, he determined not to ignore the heritage of the past.

Now it is true, as Sigerist has said, that "experience has preceded science more than once." But this is not to say that the lore of the past is not to be retested by scientific means before retention or rejection. Aschner, however, as he became more learned in medical history, seems to have become less critical of ancient beliefs regarding medical virtue and less aware of contradictory evidence from scientific experiment. He revives the ancient theory of the four humors and the use of counter-irritants. He calls for leeches, venesection, purges and emetics, hydrotherapy, sweating, and other devices for detoxicating the system. There can be little doubt that some of these treatments may in certain cases be helpful. But Aschner neither establishes statistical proof nor cares for experimental verification. Treatments are efficacious because Galen, or Paracelsus, or perchance Hippocrates, recommended them. In our author's hands, medicine becomes an art based on intuition, no longer a science.

As a result, all varieties of questionable statement and clear error abound. What is one to think of remarks such as these: "Meat, spices, and alcohol tend to make the individual 'hot-blooded' "; "overfeeding with a milk and gruel diet makes the stomach lazy and provokes hyperacidity. Forcing [children] to drink a pint and even a quart of milk a day thus greatly contributes to frequent tonsillitis"; " . . . conclusions as to constitution, character, intellectual capacity, and temperament may be drawn from a man's nasal configuration"; "a large mouth indicates greater vital energy"; "the female body . . . certainly is not as strongly differentiated from the body of the child as is the male body"; "menstruation is . . . a purge of the whole system"; "the cleansing of the body by skin respiration"? Aschner cites with approval the drugs recommended by Paracelsus for prolonging life—by Paracelsus, who lived 48 years. He speaks believingly of the extraordinary longevity of the Chinese. He is sure that the moon has a profound cosmic influence on women which it is superstition to deny. And all his beliefs are stated as facts.

Every page will evoke similar criticism. This book will undoubtedly be most pernicious in the hands of the general public. Read by doctors and biologists who can discern the false, it may have a wholesome corrective influence, like one of Aschner's own purges or emetics.

BENTLEY GLASS

SOMETHING NEW ABOUT HEALTH AND HEALING.

By P. F. Van Den Daele. The Christopher Publishing House, Boston. $3.00. 288 pp. 1944.

The author of this treatise signs himself B. S. This stands—not for what you suppose—but for Bloodless Surgeon. Hailing, apparently, from Boston, he makes one wonder just what the requirements for practising medicine in Massachusetts can possibly be, or whether they are enforced. Van Den Daele has a number of sensible ideas, he has picked up a considerable amount of standard medical knowledge, but one does not have to read far to run into such wonderful bits of anatomical lore as the following: "When the appendix becomes infected, the abdominal membrane, called the peritoneum, folds itself around the appendix and isolates it from other structures. This prevents deadly peritonitis. If, however, the patient eats, or even worse takes laxatives, the action of the peritoneum immediately stops . . ." The author thinks "streptococcus is so harmful and . . . staphylococcus is comparatively harmless" because "the one is the *cause*, the other is the *result* of infection." In spite of this conclusion, he later considers he has discovered a number of points fatal to the "germ" theory of disease.

The following story is so touchingly told that it must be related in full:

> I often think of a once happy family—father, mother and a most promising son. He was working for a concern whose president had great plans for him. The firm had already placed him at the head of his department and had decided to build a larger office for him. At that time there were some cases of diphtheria, and the boy asked me if he should take some "shots" for it. I advised him against it. I warned him that his heart, glands and general condition would suffer. I explained that it would be better to take normal health precautions. The company doctor, however, talked him into taking an antitoxin. About half a year later, the mother called me and related a sad story. The boy had changed entirely. He had become lazy, difficult to handle, and very wild. His superiors in the office had to demote him, and finally they had been compelled to actually discharge him. I waited for him to come home and then examined him. I found a wretched constitution, a weakened heart, and an irritable disposition resulting from his general condition. Later on, he became a "bootlegger," was caught and sent to prison. Both his parents died with a broken heart. This is a sad example of one who did things to his body without first investigating honestly what the after affects would be to his heart and glands.

The bloodless surgeon makes use of all sorts of treatments, from massage and chiropractic to hydrotherapy and bloodless surgery itself. The latter is credited with numerous cures of appendicitis, peritonitis, gall stones, and tumors, among other troubles, but just what it is, other than "corrective manipulations," is not explained. The list of cures is not relieved by any record of the number of patients the worthy doctor has killed.

This book is highly recommended to biologists on two grounds. It will strengthen their realization of the need for constant public education in matters of health and disease and for an active effort to raise and enforce the standards of medical licensing. Besides which, it is a masterpiece of unconscious humor.

BENTLEY GLASS

DEAFNESS AND THE DEAF IN THE UNITED STATES *Considered Primarily in Relation to Those Sometimes More or Less Erroneously Known as "Deaf-mutes."* *By Harry Best. The Macmillan Company, New York.* $6.50. xix + 675 pp. 1943.

The anticipation with which the reviewer opened this thick volume on a topic long of interest to him soon turned to disappointment. The first chapter, entitled "Causes of Deafness," is the one the reviewer is best qualified to judge. A large portion of this chapter, as also of several other chapters, consists of tabulations copied from U. S. census reports and textual repetitions of the data in the tables. In almost all instances, percentage rather than numerical figures are the only ones given. The author does not treat the data critically; furthermore, he repeats ideas long since discredited and seems to know but little about the anatomy of the organ of hearing. Certainly the chapter adds nothing to knowledge of the topic.

The six-page bibliography appended to Chapter I is not arranged alphabetically or chronologically. Numerous items give neither the name of the author nor the title of the paper and are identified merely by name of journal, volume, page, and year. Many clinical textbooks, old as well as recent ones, are included, and also a number of articles in popular magazines. The text contains no references to the items listed in the bibliography.

A geneticist who read the chapter on Heredity of Deafness was similarly disappointed in the treatment of that topic. Perhaps the sections of the book that deal with educational, economic, and social problems of the deaf are better than are those on biologic aspects of deafness, but the impression gained by the reviewer, from a hasty perusal of these sections, leads him to believe specialists in these fields also will be disappointed with this book.

The tone of the author's treatment of his topic is indicated by the following excerpts:

> p. 4, "The apparatus as a whole is a highly involved and complicated one, with its passageways, tubes, cavities, walls, partitions, fibres, and compact or solidified matter, all linked together in a finely coördinated but riveted connection." p. 388, "But the day of deliverance was at hand." p. 622, "It is high time in the history of the world that an end should be put to views that differentiate the deaf from the rest of their kind, or stigmatize or debase them. Too long have they had to suffer from misunderstandings, misapprehensions, misconceptions. Great will be their rejoicing when they receive in this respect only what is their due."

STACY R. GUILD

ELIMINATION DIETS AND THE PATIENT'S ALLERGIES. *A Handbook of Allergy.*

By Albert H. Rowe. Lea and Febiger, Philadelphia. $3.50. 256 pp. 1944.

This book is a brief resumé of allergic diseases. The first 130 pages are devoted to a critical review of the methods of diagnosis and the causes of allergy and their control. The balance of the book, 120 pages, is devoted to elimination diets. The style of the writing is rather stilted, as might be expected in a manual.

As the author is primarily concerned with foods and their relation to allergy, it is only natural that his interest should influence his discussion of other possible causes of allergic diseases. To any physician who is a disciple of Rowe, I am sure that this publication will be very helpful in the preparation of menus for patients suspected of having some food sensitivity. As the reviewer does not agree with the opinion that food plays such a major role in allergic diseases, excepting in infants, young children, and a small proportion of adults, it is natural that the opinion expressed is critical.

The manual is written with such didactic positiveness that one who is inexperienced might accept "food allergy" with the belief that the hypothetical discussions were backed by scientific proof; that the majority of human mortals are victims of one or more "food sensitivities." Unfortunately, the tendency toward a broad interpretation of the definition of allergy, accompanied by reports of cases inadequately studied and not followed for a sufficient period of time, has frequently led to undue emphasis upon the prevalence of food allergy.

It is unfortunate that allergists rarely consider the psychosomatic side of human behavior; careful laboratory studies of the gastrointestinal tract are often overlooked. Treatment of these important phases of medical disease frequently relieve the patient of his symptoms. Unfortunately, this is not the fault of the patient. He goes to his physician because of numerous digestive symptoms, and, if the medical advisor is an allergist, often "food sensitivity" is suspected as the cause of the discomfort. For a time the patient accepts such an opinion; then his symptoms, temporarily relieved, return, and permanent relief is obtained when a thorough study of his home environment and of his many mental problems is made, and when these all-important factors are adjusted.

Acceptance of Rowe's opinion unfortunately leads to errors in diagnosis, and while he is most sincere in his beliefs, the reviewer does not whole-heartedly accept them. The latter half of his book could be considerably curtailed.

LESLIE N. GAY

CANCER: *A Study for Laymen. Prepared for the Women's Field Army of The American Society for the Control of Cancer, Inc.*

Edited by Clarence C. Little. Farrar and Rinehart, Inc., New York and Toronto. Paper. 122 pp.; 2 plates. 1944.

For workers in public education on the subject of cancer this fine informative and non-technical treatment has been prepared by a corps of specialists. The first section deals with the spirit, methods, and fundamental principles of general biological research. In 46 pages a remarkably complete background for understanding the cancer problem has been provided by C. C. Little. Section II, Diagnosis and Treatment, contains brief introductory topics on the lymphatics (Florence R. Sabin), the preparation of tissue for microscopic study (Little), cancer hospitals (James Ewing), x-rays and radium (Edith Quimby), diagnosis and treatment (Lloyd E. Craver), and hormones and cancer (Howard C. Taylor, Jr.). These are followed by discussions of cancer of special organs—the skin, lips, and tongue (Hayes Martin), the breast (Frank E. Adair), the uterus (Taylor), the stomach (George T. Pack), the rectum, (George E. Brinkley), the bladder and prostate (Benjamin Barringer). Finally, the function and diseases of the thyroid gland (Wm. L. Watson), and trauma and cancer (Ewing) are considered. Section III, by Little, deals with the methods to be used by the Women's Field Army in public education on the subject. A word of special commendation should go to Jean Lorenz for the clear and graphic sketches and diagrams that illustrate the manual.

THE MARIHUANA PROBLEM IN THE CITY OF NEW YORK. *Sociological, Medical, Psychological and Pharmacological Studies.*

By the Mayor's Committee on Marihuana. The Jaques Cattell Press, Lancaster, Pa. $2.50. xii + 220 pp. 1944.

The Mayor's Committee of New York City, appointed to study the prevalence of marihuana usage in New York, set out to answer the following cogent questions: 1. To what extent is marihuana used? 2. What is the method of retail distribution? 3. What is the general attitude of the marihuana smoker toward society and toward the use of the drug? 4. What is the relationship between marihuana and eroticism? 5. What is the relationship between marihuana and crime? 6. What is the relationship between marihuana and juvenile delinquency? In the opinion of the reviewer, the committee adequately completed its stupendous task and in addition established a volume which will stand as an authoritative treatise on the pharmacology, chemistry, and sociological aspects of this intriguing drug.

The committee reported more than 500 vendors of the drug in New York City. The use was confined almost exclusively to the smoking of cigarettes. The cigarettes were smoked most frequently in company

with others in especially decorated incense-laden rooms called "tea-pads." Several hundred of these "tea-pads" were discovered in Harlem. The highest percentage of marihuana smokers was found among the black race. The investigation showed that marihuana smoking did not produce a tolerance for the drug or a true addiction with withdrawal symptoms. The sensations desired by the habitués were a feeling of contentment, inner satisfaction, and a free play of the imagination. The relation between marihuana usage and eroticism was found capricious.

The complete pharmacological and chemotherapeutic studies recorded are commendable. S. Loewe confirmed that the principal site of action of the drug is the brain and that the peripheral effects are negligible. No scientific therapeutic use of marihuana could be established.

JOHN C. KRANTZ, JR.

BUGS AND BULLETS.

By J. Breckinridge Bayne. Richard R. Smith, New York. $2.75. 256 pp. 1944.

Bayne knows little of literary style, but he has a story of absorbing interest to tell, the story of his own experiences in war-torn and typhus-ridden Roumania during and immediately after the first World War. He is justly proud of his services, for he accomplished wonders under the most adverse conditions, and no little heroism was required. Interspersed with the medical story are many anecdotes of Roumanian life and customs, many descriptions of countryside and people. The book is illustrated from the doctor's own collection of photographs. The central story of ingenious surgery and tireless combat of disease and malnutrition is of double interest in these days when history is repeating itself.

BENTLEY GLASS

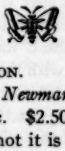
FUNDAMENTALS OF BACTERIOLOGY. *Third Edition. By Martin Frobisher. W. B. Saunders Company, Philadelphia and London.* $4.00. xvi + 824 pp. 1944.

The third edition of this book is a comprehensive text in the field of general bacteriology, including considerable related material with which the practising bacteriologist must ordinarily work—there are, for example, chapters on pathogenic protozoa and fungi. A new chapter on the pleuropneumonia group of organisms and the introduction of new discussions of aerobiology and the use of aerosols, problems of metabolism, bacteriostasis, electron and fluorescence microscopy, and other subjects of current interest and importance add much to the value of the publication. The treatment of viruses and virus diseases is a great deal more thorough than in the previous edition.

Although the book is written from a primarily medical viewpoint, it does live up to its title, in that such topics as industrial fermentations, vitamin assays, sanitary and soil bacteriology, and plant diseases are well presented. The inclusion of chapter bibliographies extends the usefulness of the text and the illustrations add to its interest as well.

In dealing with a science which has so broad a scope and in which developments are confusingly rapid, the book succeeds in being practical and informative, readable, concise and up-to-date.

HARRIETTE VERA



JAPAN'S SECRET WEAPON.

By Barclay Moon Newman. Current Publishing Company, New York. $2.50. 223 pp. 1944.

Pestilence, whether or not it is Japan's secret weapon, has certainly played a dominant role in history; it still does and will continue to do so. There is some evidence that the Nipponese have waged bacterial warfare, at least experimentally, using plague bacilli as a weapon against China. It is not, however, necessary to assume that the Philippines were captured because the Japanese took malaria there. Epidemiologists have long known that the introduction of a new population into an area tends to make them more susceptible than the native people to indigenous infections, and that malaria has been firmly established in the South Pacific for some time.

Professor Doctor Yoneji Miyagawa of the Tokyo Imperial University is said to be the diabolical inventor and director of the mass-murder program. Meanwhile, Americans have been in the throes of sleeping sickness, as evidenced by the Pearl Harbor attack and tuberculosis in New York. Contrary to Newman's opinion, scientists could hardly have been unaware of the possibilities of bacteriological warfare. Perhaps a better term would be microbiological warfare to include the various small pathogenic agents, both plant and animal, with which the "benevolent" Miyagawa is concerned.

The theses which the author presents—the possibilities and potentialities of warfare with microbes and the comparative lethargy of the American citizenry and their government in regard to their own health problems — are well founded. It is most unfortunate that the timely presentation of this material is not more logical and realistic. Emotional exaggerations and reiterations of subject matter, with excessive and poorly supported claims, tend to be unconvincing. The power of plagues needs no garnishing. In the public schools, in the press and in ordinary conversation, people customarily use rather more scientific terms without referring to disease-producing organisms as rodlets or

cocktails. A more solemn, respectful, and vigorous reminder might have made a more forceful warning.

HARRIETTE VERA

THE MICROBE MAN: *A Life of Pasteur for Children. Puffin Story Books.*

By Eleanor Doorly, with an introduction by Professor Pasteur Vallery-Radot. Penguin Books, Harmondsworth, Middlesex; New York. 9d. (paper). 112 pp. 1943.

In simple and moving language Miss Doorly has told for children the story of Pasteur, basing her account chiefly upon Vallery-Radot's biography. This is a book for all biologists to read to their children between the ages of eight and fourteen. It is a worthy introduction to the spirit of science.

THE BABY MANUAL. *A Practical Guide from Early Pregnancy through the Second Year of Life.*

By Herman N. Bundesen. Foreword by Thomas Parran. Simon and Schuster, New York. $3.00. xii + 590 pp. 1944.

Over 10,000,000 copies of the original form of this manual have been distributed. In its more extensive new version and fresh format it should be useful to many additional parents. It is simple in style and includes answers to virtually every question about baby care that even the most ignorant mother could think of asking. Its most excellent feature is its organization, which makes it possible to find desired information easily and quickly. The first two parts of the book deal respectively with prenatal care and care of the baby (feeding, clothing, bathing, sleep, fresh air, sunshine, sickness, training). The second half is in question-and-answer form, arranged according to the infant's age, beginning with the premature baby, proceeding month by month up to the age of one year, and then through the second year in periods of three, three, and six months.

YOU ARE YOUNGER THAN YOU THINK.

By Martin Gumpert. Duell, Sloan and Pearce, New York. $2.75. ix + 244 pp. 1944.

The author, an exile from Germany who is now an American citizen, discusses in remarkably clear, simple, and forthright style the problems of aging. Only for those who are not looking forward to, or dreading, the years of old age, or who have no concern for maintaining their health and vigor through the years will this book have no interest. The first part of the book is a general account of the biology of aging, of normal old age, and of the social problems of aging. The second part, an overgrown appendix as large as the body of the book, is slightly more technical, taking up the diseases of old age organ by organ, from the skin to mental disturbances. This portion will be a useful handbook for consultation as ailments develop.

The book opens with an amusing account of the founding and successful efforts of the Committee on Longevity of the class of 1900 of the College of Physicians and Surgeons of Columbia University to keep the members of their group alive and in health. Then the life-span and the ratio between age groups in the population, the connection between age and disease, longevity, the changes of aging, and physiological age and biological time are discussed. Emphasis is laid on the importance of energy-saving and of keeping up physical and mental activity. Gumpert also considers the effects of the weather, diet, stimulants, and sex activities on older persons. The account of Bogomolets' work in Russia with the antireticular cytotoxic serum (ACS) in cancer treatment, bone fracture, and rejuvenation is arresting and leads to the hope that it may soon be confirmed in this country. The author supports the philosophy of a creative old age with an abundance of instances. Altogether, he has written one of the best recent books on scientific subjects for the general public. Biologists will find it well worth their attention.

BENTLEY GLASS

HOUSING AND HEALTH. *Design for Britain (Second Series), Number 26.*

By Sir John Boyd Orr and Frank Wells. J. M. Dent and Sons, Ltd., London. 6d. (paper). 31 pp. 1944.

This is one of a series of pamphlets issued recently in Britain by the Cooperative Permanent Housing Society, and designed to stimulate thought on post-war reconstruction.

It begins with a plain statement of facts and figures on the relation between housing conditions and delinquency, the death rate, and the incidence of diseases. On the basis of further facts regarding the extent of housing requirements, a strong plea is made for giving absolute priority in labor and materials to the post-war housing program.

In order to plan housing for health it is necessary to have a master-plan—to estimate the future development of industries, to determine their location, and to build new towns or rebuild old towns in relation to industrial needs. The authors advocate postponement of such a master-plan until after the war, when it will be more possible to forecast the industrial future, and when those who have returned from the front will be able to share in the planning. A practical scheme is put forward for providing temporary housing in the interim.

There is much that is controversial in this booklet, and much that is applicable to housing in other countries.

EILEEN SUTTON GERSH

THE HOSPITAL IN MODERN SOCIETY.

Edited by Arthur C. Bachmeyer and Gerhard Hartman. The Commonwealth Fund, New York. $5.00. xiv + 768 pp. 1943.

In this collection of readings the authors have united 145 articles written by 98 authors. These contributions, which have so far been widely dispersed in different journals, actually cover the whole field of hospital science.

The general orientation of the hospital, especially in view of such new problems as hospital service plans, systematic public relations, and social service is discussed extensively. Management and financial control in general, as well as administrative details such as the problem of the trustee, the superintendent, the choice of a medical staff, nursing education, legal problems, and plant maintenance, are abundantly dealt with. Such technical questions as construction, and the handling of special departments (anesthesia, x-ray, obstetrics, laboratories, etc.) are ably explained.

The overwhelming majority of the contributions is extremely valuable and representative. A treatise composed expressly by one or only a few authors would probably have avoided a number of repetitions and rather tiresome generalities, and would have gained in clearness and compactness. On the other hand, it probably could never attain the amazing richness and manysidedness of this handbook, which is due to be a standard work in its field for quite a number of years. Extensive "References for further reading" are another valuable feature of the work. The absence of an index is regrettable.

ERWIN H. ACKERKNECHT

ANIMAL NUTRITION

LA NOVELA DE LAS VITAMINAS.

By Arturo Leon Lopez, with a prologue by Pedro Escudero. Orientacion Integral Humana, Buenos Aires. $12.00m/arg. 449 pp. 1943.

This volume might serve as a script of a movie to be entitled 'Vitamin Fantasia.' Episodes such as 'the vitamin of the motorist,' 'the vitamin of the mariner,' the vitamins of 'the nerves, of youth, of mental equilibrium, of fecundity' follow one another in breathless succession, and indicate the highly popular audience to which this book is addressed. Passing from lyrical realms that invoke Lord Byron, Brillat Savarin, and Escoffier, the dietary tables that recommend two and one-half glasses of milk daily for the adult male reviewer come as somewhat of an anticlimax. Scientific lapses, such as concern, for example, the roles of vitamins C and E, are probably not greater than ordinarily encountered in a volume of this appeal. There is plenty of historical background for the discoveries of the vitamins, in the manner of *Hunger Fighters*. The illustrations for this book are highly original, frankly 'poster art' exhibits, with here and there a hint of Dali; properly reproduced, many could serve as excellent adjuvants for school teaching and adult education. Emphasis has at least been placed on foods rather than vitamin pills. A word of cavil should be directed at the pictures of eminent investigators that adorn the book. They are reproduced so fuzzily that it is doubtful whether their own graduate students could recognize them. In conclusion, one may catch up with one's Spanish and with vitamins (the quintessence of life) by means of this entertaining book.

H. R. CATCHPOLE

INADEQUATE DIETS AND NUTRITIONAL DEFICIENCIES IN THE UNITED STATES: *Their Prevalence and Significance. Bulletin of the National Research Council Numer 109.*

Report of the Committee on Diagnosis and Pathology of Nutritional Deficiencies, Food and Nutrition Board; H. D. Krause, Chairman. National Research Council, Washington. $2.12. ii + 56 pp. 1943.

This bulletin is an excellent report of the Committee on Diagnosis and Pathology of Nutritional Deficiencies of the Food and Nutrition Board. It is a review, bringing together the results of dietary surveys and nutritional appraisal which have been scattered widely in various journals. It also includes some previously unpublished material. Some of the data have been recalculated and reclassified on a uniform, authoritative, and comparable basis.

The first division of the report is titled "The Prevalence of Inadequate Diets as shown by Surveys." This includes a discussion and table of recent standards and systems which have been used in evaluating diets. It contains also the results of surveys conducted in 1938-40 and 1940-43. The surveys were most inclusive, being made on school children and adults in all sections of the United States; on people of various income groups; on people of various races. The results are stated for each survey in percentages of the group failing to meet the daily allowances, and then the results are combined and tabulated in various ways. These are excellently done, since they show comparisons of the various groups tested. Because of the criticism that "the recommended dietary allowances presumably represent 'optimum nutrition,' and perhaps many persons who do not have the margin of safety are in no way deficient," some of the surveys have been incorporated in tables which present the

proportions of families whose diets fail to meet not only the full recommended levels for constituent nutrients, but also 75 per cent, 50 per cent, and 25 per cent of these levels. The authors say "from this scale any one can take his choice of levels as a standard." All of the surveys showed the marked prevalence of dietary inadequacies as judged by recommended standards.

The second division of the report is on "Deficiency States: Their Causes, Forms and Detections." This part discusses the point that surveys indicate only dietary deficiencies of a given period. Deficiency states due to cumulative effects are more prevalent and severe than indicated by a dietary survey, for a person's nutritional status depends on the events of all past days. Methods are being made available to detect these states.

The third division is titled "The Prevalence of Deficiency States' and summarizes (1) the recorded prevalence of severe, acute forms as obtained from (a) evidence from official mortality rates, and (b) from hospital admission rates; (2) the recorded prevalence from chemical examinations (this includes tables); (3) medical assessment of nutritional status. All of these indicate that deficiency states are common among the population of the United States.

The fourth division deals with the "Significance of Deficiency States and Optimum Nutrition." This division considers the effects of proper diet on growth and development; the effect of prenatal diet on childbearing; the effect of avitaminosis on well-being and efficiency; diet and dental caries; nutritional status in relation to susceptibility and resistance to infections; and the application of the significance of optimum nutrition.

The final division is the "Summary and Conclusions" and brings most clearly the results of the surveys—that there is a widespread prevalence of moderately deficient diets and that this presents a preventive and corrective problem.

The bulletin also contains a bibliography containing 189 references. The report is one which is excellently written. The results of the surveys are stated clearly and concisely, and sound conclusions are drawn at the end of each division. The final summary and conclusions bring together, briefly, in well chosen statements, the results of these far-reaching surveys.

MARGUERITE M. SCHMIDT

HANDBOOK OF NUTRITION. *A Symposium Prepared Under the Auspices of the Council on Foods and Nutrition of the American Medical Association.*

American Medical Association, Chicago. $2.50. 586 pp. 1943.

This excellent Symposium consists of an introduction by James S. McLester, chairman of the council, and twenty-four articles on various phases of nutrition, each article written by an authority in the field, as follows: Proteins in Nutrition, Howard B. Lewis; Role of Fat in the Diet, W. R. Bloor; Calories in Medical Practice, E. F. DuBois and W. H. Chambers; Water and Salt Requirements in Health and Disease, John H. Talbott; Principal Mineral Elements in Nutrition, I. G. Macy; Iron in Nutrition, C. W. Heath; Iodine in Nutrition, G. M. Curtis and M. B. Fertman; The Trace Elements in Nutrition, M. E. Shils and E. V. McCollum; The Fat Soluble Vitamins, Hugh R. Butt; The Water Soluble Vitamins, C. A. Elvehjem; Foods of Plant Origin, Leonard A. Maynard; Foods of Animal Origin, H. C. Sherman; Unusual Foods of High Nutritive Value, Russell M. Wilder and Thomas E. Keys; The Preservation of the Nutritive Value of Foods in Processing, Edward F. Kohman; Improving the Quality of Cheap Staple Foods, George R. Cowgill; Recommended Dietary Allowances, Food and Nutrition Board, National Research Council; The Feeding of Healthy Infants and Children, Philip C. Jeans; Feeding the Aged, Edward L. Tuohy; Nutritive Requirements in Pregnancy and Lactation, J. Harry Ebbs; Adequacy of American Diets, Hazel K. Stiebeling; Medical Evaluation of Nutritional Status, H. D. Kruse; Nutrition in Preventive Medicine, W. H. Sebrell; Conditional Malnutrition, Norman Jolliffe; Principles of Diet in the Treatment of Disease, Tom D. Spies. Each of these articles is a review of the latest literature in the field, and contains the references to the original literature at the bottom of each page. On the whole, the papers are clear, concise and to the point, covering the available information.

While space does not permit comment on all of the papers included in this handbook, a few may be given special comment: The article on proteins is a fine review of the subject, including a brief discussion of the structure, value of amino acids, dietary needs, and recent developments in protein metabolism. Butt, in his paper on "The Fat Soluble Vitamins," has given "data which it is hoped will be of value in orienting conceptions in a rapidly changing subject." The subject of the water-soluble vitamins is well summarized by Elvehjem, who includes a general summary of the more significant facts and stresses the nutritional aspects of these vitamins. Talbott has a fine review of the water and salt requirements in health and disease.

At the front of the book is a list of the contributors, giving the places with which each of them is associated. There is an excellent index. The book will be a very valuable one for anyone interested in the field, and is highly recommended.

MARGUERITE M. SCHMIDT

THE ORIGIN OF FOOD HABITS.

By H. D. Renner. Faber and Faber Ltd., London. 15s. 261 pp. 1944.

It has been increasingly realized that food habits are neither the expression of our unswerving instincts for caloric and vitamin requirements nor simply the unpredictable product of innate foolishness, as they first appeared to somewhat naive and bewildered dietitians. The book under review is one of the most interesting attempts to find new ways of understanding food habits. The approach of the author is "psychological," a term whereby he comprises two entirely different sets of motivations under a common label, namely, reactions toward food dictated by the physiology of our senses; and true mental reactions, often entirely illogical and irrational, and understandable only upon historic grounds. While the latter have found larger attention in the recent past, to emphasize the former is a particular merit of the author. That some of his physiological explanations are highly controversial and probably rationalizations of the irrational, does not detract in the least from his merits, and is unavoidable in view of the fragmentary character of our knowledge of the physiology of our senses.

The author reviews in detail the influence of climate and of original techniques in agriculture and food preservation on the formation of food habits, especially in the British Isles, as well as the changes brought about by modern manufacture and global economy.

An extraordinary wealth of data and of ideas are handled competently in this small book. Their very overflow has produced a staccato style which does not always make good reading. This minor weakness will not deter those interested from studying what is one of the most important publications in the field of food habits.

ERWIN H. ACKERKNECHT

ALL ABOUT FEEDING CHILDREN.

By Milton J. E. Senn and Phyllis Krafft Newill. Doubleday, Doran and Company, Garden City, New York. $2.50. xviii + 269 pp. 1944.

Here is a handbook on children's nutrition that is compact, well organized, and different. The first section of the book takes up needs and problems of children's nutrition according to the child's age, paying attention not only to what should be fed and how it should be prepared, but also to the importance of psychological factors. The second section is a new sort of cookbook, detailing many methods of preparing the main types of foods so as to make them appetizing to children. Parties and picnics are not forgotten, and the novel chapters on the school lunch box, on traveling with young children, and on food and the war complete an exceptionally sound and helpful book for the home. It should also be useful to dietitians in schools, hospitals, and other children's institutions.

NUTRITION AND NATIONAL HEALTH *being The Cantor Lectures delivered before The Royal Society of Arts 1936. By Major-General Sir Robert McCarrison. Faber and Faber Limited, London.* 6s. 75 pp.; 3 plates. 1944.

A reprint of three lectures delivered in 1936, this little book still provides a fundamentally sound outline of the principles of nutrition, though in a few respects it is not quite up to date (vitamin K, for instance, is not mentioned). The material is excellently presented, and it may be recommended to the general reader and to those who are concerned with nutrition in its social applications.

BIOCHEMISTRY

ADVANCES IN PROTEIN CHEMISTRY. *Volume I. Edited by M. L. Anson and John T. Edsall. Academic Press, Inc., New York.* $5.50. xi + 341 pp. 1944.

At first thought, it may seem peculiar for this kind of book to be reviewed by a histologist. Actually, the book is very stimulating to the reviewer, and should be so to morphologists generally. There are numerous indications that biochemistry and histology are coming to the point where things as seen (with the white light, ultraviolet, or electron microscopes) are to be characterized in physical and chemical terms; that is, when quantitative chemically-valid terms will be used to describe structures. This merging of the two fields is bound to catalyze cytology, for it exposes enormous possibilities for the functional interpretation of morphologic elements. These comments apply particularly to five of the eight articles included in the volume (Chargaff, "Lipoproteins"; Schmitt, "Structural Proteins of Cells and Tissues"; Greenberg, "The Interaction between the Alkali Earth Cations, Particularly Calcium and Proteins"; Greenstein, "Nucleoproteins"; Bailey, "The Proteins of Skeletal Muscle"). The remaining articles are by Treffers, "Some Contributions of Immunology to the Study of Proteins; Chow, "The Purification and Properties of Certain Protein Hormones"; and Payne and Stuart, "Soybean Protein in Human Nutrition."

Each article is accompanied by an extensive bibliography. The author and subject indices covering all articles are helpful. It is regrettable that the binding, paper, and printing are not of as high quality as the contents, because of the government's regulations for conserving paper and other materials.

I. GERSH

LABORATORY EXPERIMENTS IN BIOLOGICAL CHEMISTRY.

By James B. Sumner and G. Fred Somers. Academic Press, Inc., New York. $2.60. vi + 169 pp. 1944.

This laboratory manual has been prepared by the authors for use in their own courses, but it should be of value to many who are looking for a laboratory manual "ready to use."

The first pages of the manual contain "General Instructions." These are excellent ones for any course. They deal with "safety first regulations," "cleaning solutions," "concentration of solutions," and "preliminary training in analytical chemistry." The instructions are clearly written and very easily understood.

The manual is divided into two parts, each part for one term's work. In the first part, the experiments are grouped under the following headings: lipids; bile; acetone bodies; formaldehyde and methyl alcohol; dialysis; carbohydrates; plant pigments; determination of Vitamin C; gastric analysis; urinanalysis; blood-quantitative analysis; and electrometric determination of pH. Part II experiments are under the following headings: amino acids; proteins; hemin, hemoglobin, and related compounds; agglutination; enzymes–general, enzymes–preparation; activity determination; and alcoholic fermentation.

The experiments that have been chosen as representative ones under each of these groups are good ones. They are clearly written and most explicit. Much explanation of the reactions involved, of the precautions necessary, and of the errors that might occur are included. Questions are asked. Directions for the preparation of various solutions are given,—an excellent feature, since the student is given this information directly. Original literature references are made at many points.

The order of the experiments is an unusual one, but this is a minor criticism, since the order of performance of the experiments can be determined at will. The number of quantitative urine experiments is quite small. It is true that the authors have said in their preface that they have chosen "typical" ones. However, it is customary in most biochemistry courses to do a quantitative analysis of a 24-hour sample, and the directions for such an analysis are lacking in this manual. The number of experiments on enzymes is quite large for the average course in biochemistry. However, on a whole, the manual is an excellent one that could be readily adapted to any class.

MARGUERITE M. SCHMIDT

THE CHEMISTRY AND PHARMACY OF VEGETABLE DRUGS *Dealing with the Derivation and Properties of All the Principal Vegetable Drugs.*

By Noel L. Allport. Chemical Publishing Company, Inc., Brooklyn. $4.75. viii + 252 pp. 1944.

This treatise includes chemical, pharmaceutical, and pharmacognostic descriptions of many vegetable drugs. The author has not limited the scope of the text to the drugs recognized in the official compendia, but includes many roots, leaves, and barks that are no longer official.

The division of the subject matter is based upon the character of the drugs discussed. Thus several chapters deal with alkaloid-bearing drugs such as opium, belladonna, and cinchona. Other chapters are concerned with resinous drugs like jalap and podophyllum and senna, and other cathartics find their appropriate places in other chapters.

Each drug is introduced historically. Its pharmacognostic characters are outlined and often completely illustrated. The constituents of the plant are treated at length, with special emphasis on those which have medicinal value. The chemistry of the alkaloidal substances is included. Galenical preparations made from the crude drug or its active principles are described. The standardization of the various vegetable drugs is given in great detail, except when the assay is biological in character. In these instances the author gives only a brief outline.

The style of the author is lucid, and as one peruses the volume he reaches the conclusion that the book is an expression of the author's experience with the drugs which he discusses. Indeed, this volume is an excellent reference and guide to the pharmacist, drug control chemist, and pharmaceutical manufacturer.

JOHN C. KRANTZ, JR.

PSYCHOLOGY AND ANIMAL BEHAVIOR

THE PHYSICAL BASIS OF PERSONALITY. *Pelican Books. By V. H. Mottram. Penguin Books, Harmondsworth, Middlesex; New York.* 9d (paper). 126 pp. 1944.

In this book a description of meiosis is accompanied by the footnote: "This account, in fashion when the writer was a student, is no longer held to be true . . . ". Says Mottram: "No one would deny that sex conditions personality," and after some discussion of the justification for generalizations about sex and personality, " . . . justification or not, it hardly matters so long as there is a general agreement, which I think is undoubted, that sex conditions personality." Whereupon he presents the argument that sex (and therefore personality also) is determined by the chromosomes. "This," he writes later, "is the first and ineluctable piece of evidence that our personalities are determined by our chromosomes."

Before one looks for further evidence in his discussion of the nervous system and endocrines, one may wonder at this point why Motram was impelled to write a book on this subject, unless one has read the warning preface: "The chasm between the opposing points of view [of science and religion] must be bridged."

For more than three quarters of the book the writer plays devil's advocate for a materialist outlook—our personalities are determined by our chromosomes and

these in turn are subject to fixed laws of behavior and probability—this is all there is to it. He rejects various attempts to escape from this position through philosophical argument, and finally chooses to escape by counterposing the experience of the mystic to that of the scientist—the genes determine only the "persona," the character portrayed upon the stage. The true self of the actor cannot be apprehended by the scientist as such, but only by the mystic.

EILEEN SUTTON GERSH

THE PSYCHOLOGY OF WOMEN. *A Psychoanalytic Interpretation. Volume One.*

By Helene Deutsch. Foreword by Stanley Cobb. Grune and Stratton, New York. $4.50. xiv + 399 pp. 1944.

In this volume Helene Deutsch has brought together results of a continuing interest in what Freud referred to as "the problem of woman." Freud didn't expect woman to solve her own problem because, as he said, "You are the riddle yourselves." If he were living, he might very well confess that in this book Helene Deutsch has gone a long way to explain to many people's satisfaction many aspects of feminine psychology.

Using the psychoanalytic method, which essentially is based on the theory that the psychologic structure of the person is formed in the early years, she divides the book into three essential parts. The first deals with the young girl's psychologic development into womanhood, a process beginning in the early years and extending through puberty, in the course of which "the feminine core" is definitely formed. There are chapters on prepuberty, early puberty, puberty and adolescence, and menstruation. The second part deals with the detailed examination of this feminine core. Deutsch finds that there are three essential traits of femininity: narcissism, passivity, and masochism. Accordingly there are chapters on eroticism: the feminine woman, in which are described three types of the feminine woman; feminine passivity; and feminine masochism. In the third part certain types of women who do not appear on the surface to fit into the three feminine types are described. Accordingly there are chapters on the "active" woman; the masculinity complex; and on homosexuality. Finally there is a chapter on the influence of the environment on feminine psychology. The book ends with a bibliography and index.

It is impossible to give in detail the gist of the observations and theories exposed in this book. The author draws on a vast experience in dealing with girls and women of all ages, and because of the wealth of her material what she has to say carries the ring of authenticity. This reviewer is less impressed with her use of material from belles-lettres. It may or may not be true, as she insists, that such material, while less objective, is "all the more true because more inspired." It is quite possible that the author has taken too literally to heart her own deduction concerning woman, that her strong point is intuition, not logical reasoning. This reviewer, being a male, would have preferred that she stick to clinical material. To build up a theory and then to argue its worth on the basis of a mythical construction from someone's imagination does violence to my scientific training. The mythical construction might be all she says it is; again it might not. By contrast she makes very telling use of hospital records, and, it may be noted, not her records, but records taken by other people and used for all they were worth to illustrate her points.

Speaking generally, Deutsch would say that women are different psychologically from men in their greater capacity for emotion, in their use of emotion, and, perhaps related to this, in their use of intuition to arrive at understanding rather than by cold logical reasoning. In fact, she feels that really feminine women do not approach men in their intellectual processes, but are vastly superior in their empathic potentialities.

Here and there through the text she has deviated slightly from the true Freudian doctrine, and these deviations seem well supported by her own observations, but for the most part she follows strictly Freudian doctrine, including penis envy as a fundamental of all womankind. She says this is so regularly found in analysis that it may be assumed as the universal phenomenon. This is one of the points where a traditional but enlightened psychiatrist would question whether the reputed universality of the findings is as much the consequence of the use of analytic method as of the intrusion of analytic dogma into the findings.

Deutsch concludes that women are by nature monogamous, but there must be better reasons for concluding this than some she advances. For instance, she alludes to the distress of a girl over the questionable fatherhood of her child. This child was born in a country where the fatherhood of the child is said to be of no social consequence, but the author glides over the fact that her contact with the girl was in a country where such a state of affairs obviously did not exist. How much the girl's distress was due to environmental factors is not stated. Was intuition at work in the author here?

It is, however, not the wish of this reviewer to carp at a few things which rub him the wrong way. The volume obviously is full of factual information which anyone would be glad to possess.

The author promises a second book having to do with "the central problem of feminity—motherhood." The first volume therefore deals with the development of the individual woman's personality, and the second volume will deal with her as a servant of the species. If the second volume is as provocative of thought as this one, then the author will have furnished an important and well rounded contribution toward a matter

of importance to all psychiatrists, to say the least, and conceivably to all women and men.

WENDELL MUNCIE

RORSCHACH'S TEST. *I. Basic Processes.*

By Samuel J. Beck. Foreword by Willard L. Valentine. Grune and Stratton, New York. $3.50. xiii + 223 pp. 1944.

In this book Beck demonstrates exactly how to go about the evaluation of the Rorschach test responses by the use of a few examples examined in detail. He follows very closely Rorschach's original work, adopting the English symbols used in the Lemkau-Kronenberg translation of "Psychodiagnostik." The book will be found very useful to Rorschach testers.

WENDELL MUNCIE

SOCIAL PSYCHOLOGY. *Second Edition.*

By Kimball Young. F. S. Crofts and Company, Inc., New York. $4.00. viii + 578 pp. 1944.

Those who are acquainted with the scholarship, thoroughness, and readability of the first edition of Young's *Social Psychology* will welcome this new edition, equally interesting and stimulating, with some chapters expanded and others wholly new.

The pre-human sources of social interaction, in the social life of lower animals, especially monkeys and apes, are presented in the second chapter. The next, on Culture and Personality, includes a six-page comparison, in columns, of the principal cultural factors of eight selected native peoples, and a three-page comparison of such features of Japanese, Germans, and Americans. Two chapters deal with the elements and mechanisms entering into the rise of the social self, with a clear and appreciative exposition of George H. Mead's theory of the "I" and the "Me," an elaboration upon the concepts of William James, Josiah Royce, J. M. Baldwin, and Charles H. Cooley. The treatment of social cultural reality has been extended. In trying to meet the needs of a better understanding of past and present national psychology, the author has added one chapter on the psychology of revolution and two on war and wartime morale. The importance of the motion picture and of radio have received increased attention, in the treatment of public opinion. Two chapters are devoted to propaganda, with special attention to the two World Wars; and, finally, the nature and the use of power are discussed as pertinent to the revolutionary threat to democratic culture and the facts of total war.

The format is good; the style is clear, easy, and attractive. Suggestions for further reading are provided for each chapter. An index of names as well as of subjects is given. This edition is entitled to a place among the most popular and valuable textbooks in social psychology.

WAR NEUROSES IN NORTH AFRICA. *The Tunisian Campaign (January–May 1943).*

By Lt. Col. Roy R. Grinker and Capt. John P. Spiegel. Prepared and distributed for The Air Surgeon Army Air Forces by the Josiah Macy, Jr. Foundation, New York. Paper. 300 pp. 1943.

This book has finally been taken off the restricted list by the Air Surgeon of the Army Air Forces. The authors discuss their experiences with war neuroses in the Tunisian campaign. The book is heavily documented with case records of the following clinical syndromes—free-floating anxiety states, both severe and mild, somatic regressions, psychosomatic visceral disturbances, conversion states, depressed states, concussion states, exhaustion states, psychotic states, and malingering. Furthermore there are chapters on the special psychiatric problems in the Air Forces both among ground and flying personnel, with examination into their etiology from the constitutional standpoint, from the standpoint of previous neurotic trends, of sociological factors, physical state, and psychological factors. There are further chapters on treatment procedures, of which the most interesting, because the newest, is what the authors call narcosynthesis, reliving of the traumatic experience under pentothal sodium narcosis with an active part being played by the physician, who enacts whatever role the drama demands in the interests of a better synthesis of the patient's ego. Psychotherapy, convulsive shock treatment, continuous sleep as well as other standard procedures are also discussed briefly. There is a final chapter on psychodynamics, with topics on factors augmenting anxiety, factors protective against anxiety, conditions breaking down the capacity for handling anxiety, the dynamic struggle of the ego with anxiety, psychobiological mechanisms, the dynamic source of various symptoms of the war neuroses, the dynamic effect of narcosynthesis and psychotherapy, and the reconstructed ego and its vicissitudes.

It is a thrilling experience to read this book, and one is grateful to the authors for presenting the material so forcefully. The various reaction types have been described in numerous papers from the British Isles as well as by the military service of the U. S. Army and Navy, and there may be nothing new in these descriptions, but at least the descriptions are wonderfully done. There are only a few comments which the reviewer as a civilian psychiatrist would feel prompted to make. In the first place, the book has a distinctly psychoanalytic flavor, as is to be expected from its authorship. This bias goes a little far perhaps when, for example, in the course of discussing a patient with hysterical conversion manifestations the authors state,

"The libidinal component in the hysterical conversion states could not be determined by us in the time available. The all pervading reality of the war situation so dominates the clinical picture that unconscious erotic factors are difficult to discern." (p. 59). The implicit assumption here is that the hysterical conversion states must have a libidinal component, and that there is no other proper final explanation of these states. This may or may not be true despite analytic dogma. Likewise, "Severe conflict over hostility is indicative of chronic neurosis." (p. 146). It is certainly true that a great many chronic neurotics display much hostility, as the authors go on to state, but that this is an indication of chronic neurosis remains to be proven.

Especially interesting was the confusion (not of the authors apparently) in the original diagnosis of certain states of acute and severe free-floating anxiety with schizophrenia. These several cases described by the authors came to them with an initial diagnosis of schizophrenia. The authors state, "It is our opinion, however, that prior to the institution of therapy, this condition (severe anxiety) may be distinguished from schizophrenia by the quantity of anxiety exhibited by the patient." Also, "Differential diagnosis from schizophrenia often can only be made by a therapeutic test with intravenous sodium amytal or sodium pentothal, to which the anxiety states respond promptly and dramatically." To this reviewer there is a certain underlying inadequacy in this attitude toward differential diagnosis. Plainly these patients were in panic, and panic has very much the same character as delirium, in the sense that when present it is apt to cover over the underlying personality so completely that it is impossible to state whether one is seeing panic in a formerly and basically well adjusted person or panic in a person with a disrupted personality. We were always taught that when panic is present it is best simply to make that diagnosis and wait for the further eventualities to see what underlies the panic. The use of sodium pentothal as a differential diagnostic feature, however, is important in this situation and corresponds roughly with the massive sedation used in civilian panic states, out of which any kind of personality may emerge. It is no tribute to the teaching of psychiatry in this country that this fundamental fact should be so misunderstood.

The authors are at their best and most dramatic in describing their success with narcosynthesis. This evidently has been a very valuable therapeutic agent, and by its use has thrown a great deal of light on the actual mechanisms involved in the production of war neuroses and in their alleviation. For this, if for nothing else, every practicing psychiatrist could be grateful to the authors.

WENDELL MUNCIE

THE WAR AND MENTAL HEALTH IN ENGLAND.
By James M. Mackintosh. The Commonwealth Fund, New York. 85 cents. 91 pp. 1944.

The author has given a very lucid account of the problems of mental health in Great Britain. The book is divided into two parts—Part I, The Impact of War, and Part II, Mobilization for Peace. In Part I the reader is taken through the process of adjustment in going from peace to wartime status, through the "lonely year 1940–41," through preparations for the final blows, and "the end of the beginning, 1942–43." Material of this same sort has appeared in various accounts from overseas. Particularly interesting is the story of the evacuation of the children and the problems raised by this procedure, problems which will not end with the coming of peace. Interesting also is the boost to the general morale with the declaration of war, the inability of the common people to accept defeat, and the dogged persistence of preparation for the final onslaught. The author touches rather guardedly and lightly on the problems raised by the American use of England as an advanced base.

In Part II Mackintosh discusses the hospital services, the voluntary organizations for mental health, professional education in mental health, and some problems of the future. Already a great deal has been accomplished in Britain in these years through the military and civilian governmental organizations in rehabilitation, but the author looks forward to something better than rehabilitation. He looks forward to professional and lay education in the abundant use of assets in the maintenance of mental health and the prevention of mental breakdown. He envisages, for example, the establishment of preventive health institutions in which there will be basic training, including basic training in mental health with an opportunity for specialization later on, courses open to physicians and to nurses.

Altogether, this is a stimulating book interspersed with humorous bits, and even the story of the most trying years is not a lugubrious thing.

WENDELL MUNCIE

MILITARY PSYCHOLOGY.
By Norman C. Meier. Foreword by Lieutenant General Ben Lear. Harper and Brothers, New York and London. $3.00. xx + 395 pp. 1944.

This book is an excellent presentation of military psychology divided into Part I—General Principles and Practices, and Part II, Applications and Problems. A full and adequate glossary of 13 pages concludes Part II. One may think of the eight chapters as falling into four groups: A. Social Psychology: Group Conflict, Combat Psychology, Preparation for Morale Combat; B. Educational: Adaptation of Skills to Military Needs,

and Learning Military Skills; C. Leadership: Leadership and Coordination, Leadership in Combat Situations; D. Abnormal and Adjustment Psychology: Adjustment to Combat Conditions and Stress.

The author does not give us arm-chair, theoretical psychology but principles and practices based on research and investigation in social psychology, the psychology of World War I and World War II, the psychology of skills and abilities, perception and deception (camouflage), learning, forgetting, teaching and study, and medical and abnormal psychology. The author has not only placed important facts and principles at the disposal of the military forces, but has made available to teachers, public servants, and lay readers many interesting and useful facts concerning the various phases of military psychology, personnel, morale, camouflage, and preventive and remedial mental hygiene.

The style is clear, interesting, attractive. The book is highly informing. All who have relatives and friends in the war will find this a valuable book, one which will help them to appreciate the psychological factors with which military officials, servicemen, psychologists, psychiatrists, and civilians have to deal during the remainder of this war and in many ways after the war. And, it goes without saying, the book is the outstanding textbook on military psychology, being very highly recommended by Lieutenant General Ben Lear of the United States Army.

In Part II there are applications and problems for each of the chapters in Part I. There are also four appendices: A. Suggestions for Handling Interviews; B. Requirements for Miscellaneous Services; C. A Rating Scale for Candidates for Officers Training Schools; and D. Proposed Additional Methods for Selection of Combat Officers. The glossary follows these divisions. There is also an index.

C. HART WESTBROOK

NORMAL LIVES FOR THE DISABLED.

By Edna Yost in collaboration with Lillian M. Gilbreth. The Macmillan Company, New York. $2.50. x + 298 pp. 1944.

This is an enlightening, human, inspiring book. The facts and techniques needed by the handicapped are well, fully, and clearly presented. But the philosophy of how to take misfortune and to convert it into an asset, of how to achieve a happy and useful life when the world may seem to have crashed about one, is even more valuable to the reader than the well chosen details of how to prepare for a job and to find and hold it.

The style is direct—the writer speaks directly to the reader; and if he has any human feeling at all, the reader will find the book engaging. Not only the physically handicapped veterans and civilians, but thousands of other men and women who are mentally and emotionally broken as a result of long and inhumane internments will find inspiration and help as they travel the long way back to normal health (if that be possible) and to a satisfying and useful place in the economic and vocational life in the homeland.

The employers of all such handicapped persons, the relatives and friends who wish to help them but find it too difficult a task, teachers, social workers, and mental hygenists—and others, too—will find this presentation a valuable guide in their relationship with returning veterans and civilians from the warring countries of the world.

The treatment is a factual one enriched by the wide and specialized knowledge and experience of the author and her collaborator, both of whom are well known to those acquainted with human engineering in this country.

C. HART WESTBROOK

PSYCHOANALYSIS TODAY.

Edited by Sandor Lorand. International University Press, New York. $6.00. xvi + 404 pp. 1944.

This is a compendium at the hands of twenty-nine different contributors concerning various aspects of psychoanalysis as it stands today. The list of contributions is as follows: Freud's influence on medicine, psychoanalysis and internal medicine, psychosomatic medicine, therapeutic approach to psychosomatic problems, child analysis, the early development of conscience in the child, child-parent relationship, prevention of mental disease in childhood, juvenile delinquency, psychoanalytic social work, mental hygiene, development of the ego-psychology, dream mechanisms and interpretations, sexuality and its role in the neuroses, hysterias and phobias, obsessional neuroses, character formation, pathological character formation, war neurosis, neuroses and psychoses, manic-depressive psychoses, schizophrenias, organic psychoses, the technique of psychosomatic therapy, psychotherapy and psychoanalysis, the psychology of religion, psychoanalysis and sociology, problems of crime, approaches to art, psychoanalysis and literature, psychoanalysis and anthropology. The chapters are short, from ten to fifteen pages, and give a bird's-eye view of each of the topics mentioned above. As with any compendium, the contributions range from the most conservative, sound, and sane to those exhibiting a considerable uninhibited enthusiasm, to say the least. As an example of the former there is Monroe A. Meyer's "Dream Mechanisms and Interpretations," a paper which came out some time ago but which has been included because of its fundamental importance. As a minor example of the latter there is the example given by English in "Therapeutic Approach to Psycho-

somatic Problems" of the dynamic aspects of anorexia nervosa. English asserts that in this condition the dynamics will finally show that the patient is afraid to eat because she is afraid of becoming pregnant, or that by refusing food she is refusing love or sexuality, and that she actually wants to bite her mother's breasts or father's penis. English's suggestion that the physician must either carry through with the patient as best he may the matter of such dynamics, or be reduced to vitamine and iron injection, seems to leave out of account a middle course where one works with what the patient offers, with the intention of increasing the area of common interest and understanding without the intrusion of special interpretation. If it ends up with such a formulation, all right. If it doesn't (and such patients do get well without such interpretations), this ought to be allowable, too.

Where were Menninger, Rado, Horney, Kubie, and others when the assignments were made?

WENDELL MUNCIE

FREUD'S CONTRIBUTION TO PSYCHIATRY.

By A. A. Brill. W. W. Norton and Company, New York. $2.75. 244 pp. 1944.

Brill, who was directly responsible for the introduction of Freud's work and teachings into this country and who has been an active and revered figure in the psychoanalytic movement ever since its inception here, gives in this book a very dramatic and personal account of Freud's discoveries, his methods of work, and his wide-flung interests. No one will deny the enrichment that has come to psychiatry, to psychology, anthropology, and religious thought through Freud's teachings, and even the lay reader would get from Brill's presentation an easily understandable and telling account. The book is liberally sprinkled with references to Brill which are not in the least annoying, since Brill's warm, democratic, and humorous, although serious nature stands out always. As an epitome of Freud's work this reviewer has read none better.

WENDELL MUNCIE

HUMAN BIOLOGY

ENOUGH AND TO SPARE: *Mother Earth Can Nourish Every Man in Freedom.*

By Kirtley F. Mather. Harper and Brothers, New York; London. $2.00. 186 pp. 1944.

In this small book Harvard's eminent geologist takes a broad look at the problems of human subsistence and finds the fundamental facts grounds for considerable long-range optimism. This does not mean that there is not a "critical question" facing the present century; but Mather is confident that the question is not that bogey of exhausted resources and teeming populations commonly reared. The real issue is whether or not man will have the intelligence to recognize the interdependence of nations and to organize the use of resources on a world-wide scale; whether or not he will find the courage to control not only waste and spoliation but to tackle the problems of population growth with insight and resolution.

This rebuttal of neo-Malthusianism makes out a good case for the abundance of resources (enough of those non-renewable to last 1000 years) for an eventual world population of 28 to 32 hundred millions. The latter figure is based on the assumptions that present population trends will continue and that in yellow, brown, and black peoples they will have the same general character as in whites, though delayed some decades. If we accept these assumptions, the main conclusion follows,—although one may have an uneasy feeling that the author has played down the problem of diminishing returns for labor expended, both in agriculture and in the use of mineral resources, as the richer lands are occupied and the richer stores of ore and fuel are exhausted. Here the hand of science must find a way.

Mather dismisses long-range Malthusianism as an unreal specter, but there is still the very real dilemma that faces mankind in the immediate future in many parts of the world. It is doubtful, according to Warren Thompson, whether in China and India, for example, any significant decline in the birthrate is to be expected for half a century. With a declining death rate already evident, an enormous increase in population is to be expected in the remainder of the present century, barring Malthusian elimination or emigration. To anyone who knows China the view that the Chinese will be able to "find their own salvation by more intelligent adjustments of their own cultures to their resources" (Mather, *Science*, 101:199) will seem overoptimistic. Changing the fundamental culture pattern of an Asiatic people will take considerably longer than will the rapid increase of population. Resistance to methods of birth control on account of religion and outlook, and the ignorance and poverty of the masses that militate against their effective use are well-nigh insurmountable. Mather realizes all this, but his emphasis on long-range, world-wide aspects of the problem tends to minimize them.

The second half of the book is devoted to the consideration of the "critical question." Can activities be coordinated internationally? Should we take the alternative of regimentation or that of democracy? Mather's answer is unequivocally in favor of the latter, which he maintains is more efficient as well as more in accord with human nature. A slight weakness in his argument at this point is that he makes frequent comparisons between the totalitarian countries—Germany, Italy, Japan—and the democracies, especially the United States, but ignores the position of regimented Russia or of the futile pre-war democracy of France.

If it is true that "today the intellectual resources of the totalitarian nations are distinctly inferior to those of the democracies. Mental ability has deteriorated seriously under regimentation," where, as a friend of Russia, does he place the U. S. S. R.?

In the main, this portion of the book presents views that parallel to a remarkable degree those of Julian Huxley recently set forth in *On Living in a Revolution* and elsewhere. "The revolution of our times involves the transition from intellectual anarchy to international order and the advance from an uncontrolled, competitive economy to a regulated co-operative economy"—is certainly as characteristic of Huxley's analysis as of Mather's.

Mather's style is forceful, clear, and readable; his subject is one to which all Americans should give attention. It is not the intention of this reviewer to carp, for, if the book's black is so very black and its white so very white, it is nevertheless a most stimulating analysis. No reviewer could dismiss it with a scant mention.

BENTLEY GLASS

THE BRUSH FOUNDATION STUDY OF CHILD GROWTH AND DEVELOPMENT II. PHYSICAL GROWTH AND DEVELOPMENT. *Monographs of the Society for Research in Child Development, Volume IX, Number 1. (Serial No. 37).*

By Katherine Simmons. Society for Research in Child Development, National Research Council, Washington. $1.50 (paper). xvii + 87 pp. 1944.

Over a period of many years the late Prof. T. W. Todd organized and directed intensive studies on the normal physical growth and development of children. The present monograph is one of the results of these broad investigations. It deals chiefly with the anthropometric data collected on 999 white children in Cleveland whose parents are of North European ancestry and of above-average economic level. The examinations of these children were undertaken at frequent and regular intervals from birth to 17 years. The data which have here been analyzed statistically approach closely to the best that can be desired, and hence this report contributes unusually reliable cross-sectional age-sex constants for 25 anthropometric dimensions and for assessments of skeletal age during the entire period of active growth. All the many detailed findings are clearly discussed in the text and fully shown by means of tables and graphs. Of the conclusions, the following might specially interest all those with faith in popular age-height-weight charts: "The 'normal' weights found in height-weight-age tables approximate the truly normal only when height is not composed excessively of either leg length or trunk length and when ratings of body breadth are in harmony with ratings of body length."

ADOLPH H. SCHULTZ

WOMEN AND MEN.

By Amram Scheinfeld. Harcourt, Brace and Company, New York. $3.50. xx + 453 pp. 1944.

In spite of its lurid dust jacket, this is a sound, well balanced treatment of the subject of sex differences. The author has written a better book than *You and Heredity*, for while his former best seller was accurate and original, this one adds a thorough documentation of source material, and its style, while still breezy, avoids the charge of sensationalism. It is annoying, however, to find Nature personified throughout.

As a synthesis of genetic, anthropological, and sociological findings, *Women and Men* has not been surpassed. By starting with the biological bases of reproduction, sex determination, and sex linkage, Scheinfeld supplies the outstanding lack of Havelock Ellis' now classical works on sex. The extensive data on the comparative growth and development of pre-adolescents gathered in the past ten years has been summarized and evaluated in several chapters. The emphasis on the male as, although the stronger, yet the more delicate sex will be new to many readers, but is quite sound. Scheinfeld brings out the basic sex differences in intelligence tests, the effect of which on the measurement of the I.Q. is suppressed by the design of the tests and the selection of items. Puberty is discussed, and emphasis is placed on its average arrival two to three years earlier in girls than in boys, thus affecting social relations and marriage between different age groups, and education. "Not only is the girl less intellectually mature when important social problems confront her, but her errors, missteps, or transgressions may have far more serious consequences."

Adult sex differences are also discussed first from the biological point of view, ranging from hormones, skeleton, and fingerprints to disease resistance and susceptibility, and life expectancy. As to behavior, the emphasis falls on its conditioning because of physical differences, and the consequent progressive divergence of behavior patterns with increasing age. Sex life and homosexuality, crime and punishment for crime, dress, the division of labor, achievement and genius are successively considered from this point of view. The author regards male dominance and chivalry as having roots in pre-human behavior, and equality for women, in a literal sense, as both undesirable and impossible. The outcome of the Soviet experiment has helped to show that a double standard is inevitable, as long as only women bear children. Yet Scheinfeld is not biased. He does not regard a double standard as implying inferiority or justifying underprivilege on either side, and concludes with advice that takes cognizance of the difference between mothers and childless women in the society of today.

Every college student should be required to read this book. Every intelligent man and woman will find it instructive and thought-provoking. It should have a great and a prolonged influence.

BENTLEY GLASS

ENVIRONMENT, RACE, AND MIGRATION. *Fundamentals of Human Distribution: With Special Sections on Racial Classification; and Settlement in Canada and Australia. By Griffith Taylor. The University of Toronto Press, Toronto.* $3.50. xv + 483 pp. 1937.

This is in reality several books in one, as is indicated by its subtitle. It is composed of much previously published material, with some additions. As Taylor states in his preface, it is in a sense a new edition of his *Environment and Race*, published in 1927.

Fully half of the book deals with the problems of racial classification. Taylor's contribution is the application of the theory of age and area to the races of mankind. He conceives of mankind evolving in central Asia, with races spreading out therefrom like ripples caused by a stone cast into a pool. The first waves are primitive, the later progressively more evolved. By pointing to the geographic position of the various races of mankind, he is then able to place them in a series from the most primitive (Negrito) successively through Negro-Melanesian, pre-Dravidian-Australoid, and Mediterranean, to Alpine-Mongoloid. This last race, he points out, is the latest development in Asia, and is therefore the highest form of man yet evolved. By extension of his reasoning, any race in a refuge area is an early and biologically primitive race. He advocates the use of geographic location as a trait in racial classification of equal value to the usual biological characters!

Taylor's discussion and mapping of the distribution of the races is always interesting and often stimulating. There is sufficient truth in the doctrine of age and area, and in the significance of the zoning of races that Taylor's work can not be summarily dismissed. Many, however, will wish that the author showed a broader understanding both of physical and cultural anthropology. Few will be willing to accept the doctrine of all evolution of man occurring in Central Asia. Few indeed will be willing to accept his ranking of races as biologically superior and inferior; least of all on the inadequate data presented. For example, according to Taylor a primary measure of racial superiority is survival, thus, the extinction of the stone age Tasmanians by the iron age Englishmen is proof of the biological superiority of the Englishmen.

The entire book, but especially those sections dealing with racial questions is pervaded with geographic-environmentalism. Huntington's theories of stimulating mid-latitude climates versus stagnating low-latitude climates are followed and elaborated. The relationship between temperature and mental and physical energy is considered proved. Huntington's map showing mortality in the United States is reproduced to help prove the effects of good and bad temperatures. However, close comparison of the mortality map with maps of such climatic factors as seasonal temperatures, rainfall, sunshine, etc., actually shows there is no correlation. Furthermore, other mortality tables give utterly different distributions.

Taylor's handling of physical data so as to achieve a fit with cultural data is well exemplified in his development of an index, the econograph, for measuring the potential occupation of regions. On page 439 he states that by trial-and-error juggling of the weighting principally of temperature and rainfall figures he achieved what was to his mind a ratio that gave a good fit with the observable population densities in fully developed regions. On page 448, the validity of this measure is assumed to be established because it fits a fully developed region. But this is shooting your decoys and proves nothing. In practice, the econograph figures give such startling results as placing Southern California and the Congo in the same class.

The book is biologically and culturally unsound. Taylor's geomorphology and climatology are good. His attempts to go from that base into biology, anthropology, linguistics, human geography, and the prediction of future populations are highly unconvincing.

GEORGE CARTER

THE ANTHROPOLOGY OF KODIAK ISLAND. *By Aleš Hrdlička. The Wistar Institute of Anatomy and Biology, Philadelphia.* $5.00. xix + 486 pp. 1944.

The late, distinguished author had undertaken a systematic anthropological survey of Alaska during ten summers between 1926 and 1938, measuring living natives and excavating skeletal remains of their predecessors. He soon had reached the conclusion that human migration from eastern Asia to the New World had been a continuous process extending over thousands of years, and had included a variety of physical types and of material cultures. These migration waves hardly penetrated the inhospitable Alaskan mainland, but followed preferably the more inviting coastal region southwards. On the latter route the large Kodiak Island with its comparatively mild climate and good food resources appeared as one of the most promising places for the anthropological explorer. When the Russians discovered the island in the middle of the eighteenth century, they found it populated by a large tribe, the Koniags, numbering about 10,000.

Hrdlička's field work, concentrated on Kodiak Island from 1931 to 1937, produced the results he had hoped for in the form of skeletal and cultural material and permitted many conclusions concerning the racial history of southwestern Alaska and of Kodiak in particular. As early as post-glacial conditions made it possible, the island became inhabited by man. First came the Pre-Koniags, early Asiatic immigrants, resembling somewhat Eskimos and more so Algonquin Indians, but culturally a group of its own. They were remarkably uniform in type and brought with them a chipped-stone culture and a high artistic ability. They fashioned ornate stone lamps and fine bone plates, they buried

their dead, but they also seem to have practised cannibalism. They occupied the island for perhaps twelve to fifteen centuries during which time their culture gradually changed, though remaining distinctive. In Hrdlička's words, "They, however, rather degenerated in some ways, eventually fighting and massacring their own kind..." At a more recent epoch these ancient inhabitants disappeared, to become replaced by the Koniags, a cruder people, less artistic, but not cannibalistic. Physically the Koniags fall between the Aleuts and the southern Alaska Indians, with whom they form a single group which is derived by the author from the large Tungus stock of northeastern Asia.

The first part of the volume collects historical data concerning the people of Kodiak Island, their appearance and mode of life in the early Russian days. A short, second part describes the author's surveys of the island and the neighboring mainland. The record of these pioneering efforts will benefit future archeologists. The large, third part is devoted to Hrdlička's actual excavations on the island, discussing not only significant finds in detail, but describing also the daily occurrences during the field work, diary notes on weather, food, insect pests, and on all the many disappointments and thrills connected with exploring. The fourth and scientifically most valuable part (79 pages) records the physical anthropological data on the few living remnants of Koniags and on the rich collection of skeletal remains of these islanders and of their precursors.

The book is generously illustrated with more than two hundred photographs, of which those taken in the field are mostly amateurish and somewhat disappointing. This posthumous publication is of value not only to the author's professional colleagues, but also to that rapidly growing number of people interested in Alaska, the conditions of life to be encountered there, and the history of its early inhabitants.

ADOLPH H. SCHULTZ

THE CONFLICT BETWEEN THE CALIFORNIA INDIAN AND WHITE CIVILIZATION: *I. The Indian Versus the Spanish Mission. II. The Physical and Demographic Reaction of the Non-mission Indians in Colonial and Provincial California. III. The American Invasion, 1848–1870. IV. Trends in Marriage and Divorce Since 1850. Ibero-Americana: 21–24.*

By S. F. Cook. University of California Press, Berkeley and Los Angeles. $2.00; 50 cents; $1.25; 35 cents (paper). 194 pp.; 55 pp.; 115 pp.; 29 pp. 1944.

This series of essays in ecology and human biology examines the reaction of a primitive population to a new and disturbing environment, in quantitative terms. The most obvious result of the white invasion of California is the tremendous decline in the aboriginal population. In the Spanish missions, in the course of about 60 years, a reduction of 72 per cent took place. The wild tribes in contact with the Spaniards lost "only" 62 per cent. In the early American period (1848–1865) the annual rate of depletion even rose threefold, as compared to the Spanish-Mexican years. Disease accounted for 60 per cent of the losses, armed conflict for only 11.5 per cent. Dietary maladjustment is difficult to assess, and in this field the compensatory reactions of the Indians (cattle-theft, gathering of wild foods, use of white waste material) were perhaps most successful. The problems created by imposing absolutely new values in the field of labor and sex on a primitive population (including the wholesale rape of Indian women during the early American years) are duly analyzed by the author.

It is impossible to do justice in a short review to this pioneer effort, equally important for the anthropologist and the human biologist. For at least one region the great tragedy of the destruction of an aboriginal population by whites is lifted from a merely descriptive level to one of fruitful and exact scientific analysis. With great ingenuity sound quantitative material is traced and combined. The author's attempt to describe in purely biological terms processes which, at least at the present stage of our knowledge and in the author's own opinion, are not purely biological, leads sometimes to stylistic oddities which are of but minor importance.

From an editorial point of view, it is hard to understand why the first three essays have not been published as the one single volume which they actually form. Essay No. IV is an interesting short paper on the changes in Indian marital mores under the impact of white civilization.

ERWIN H. ACKERKNECHT

THE NAVAHO DOOR. *An Introduction to Navaho Life. By Alexander H. Leighton and Dorothea C. Leighton. Harvard University Press, Cambridge.* $4.00. xviii + 149 pp.; 33 plates. 1944.

This little book is destined to give to Indian Service workers a better understanding of the mentality of the Navaho, at present the largest Indian tribe in the United States (50,000 members), and to teach better methods in bringing our type of civilization to a minority with an entirely different cultural tradition. It describes the environmental, historical, and ideological background of the Navahos. It sketches the present administrative setup. The authors outline, on the basis of their own rich personal experience, methods for getting the Navaho to accept white medical care in the hospital and out-patient work without coercion, and to use elements of his own cultural legacy. Three Navaho life histories illustrate the more general statements of the authors, and are of great documentary value.

The book, well written and splendidly illustrated,

will find interest far beyond the circle of Indian Service workers. It is important to all those working on minority problems. It is most valuable reading for the professional social anthropologist. As a matter of fact, this study by two psychiatrists is one of the best anthropological publications of the last several years.

ERWIN H. ACKERKNECHT

RACIAL PREHISTORY IN THE SOUTHWEST AND THE HAWIKUH ZUNIS. *Papers of the Peabody Museum of American Archaeology and Ethnology, Harvard University, Volume XXIII, Number 1.*

By Carl C. Seltzer. Peabody Museum of American Archaeology and Ethnology, Cambridge. 75 cents (paper). vii + 37 pp. 1944.

An analysis of skulls of the Old Zuni Hawikuh, a sixteenth century Indian group, showed the physical type to be of a highly distinctive character. The distinctive features were small-headedness, short skull lengths, narrow skull widths (cranial index bordering on the dolichocephalic side of mesocephaly), high skull vaults, long total facial and upper facial heights, narrow facial widths.

These characters were distinctive enough to encourage the author to try to find other Southwestern groups of similar type. Comparisons were made with three Basket Maker groups: Grand Gulch, Arizona Basket Makers, and Hooton's "Basket Maker" segregates from the Pecos material. The first two groups are of considerable antiquity and represent the people who held the Southwest from at least the time of Christ and probably for a long prior period. The relationships between the groups was shown to be very close. The Grand Gulch Basket Makers and the Zuni are shown to be nearly identical in sixteen measurements and eight indices. Similarly, striking resemblances were shown for the other groups.

The comparisons were then extended, and the Zuni skull series was compared with skulls from Salt River Valley, Chaco Canyon, Petrified Forest, Chaves Pass, and Puyé. In comparing these groups, composed entirely of artificially deformed crania, with the Zunis it was necessary to omit the dimensions of the skull vault and to resort to the diameters and proportions of the facial skeleton, skull base, and expressions of general head size. The result was the demonstration that the Zuni were not a unique type, but that they represented a type widely distributed in the Puebloan Southwest. It is equally clear that this type is the ancient type in the Southwest, and has persisted with little change. Further comparisons, particularly with Hooton's work at Pecos on the eastern side of the Pueblo area, showed that the only evidence for sweeping changes in physical type came very late in the Pueblo period and was seemingly due to an influx of peoples from the Plains area to the north and east.

These findings are at complete variance with the American anthropologists' long established dogma of the occurrence of a sweeping change in physical type at the time of the cultural shift from Basket Maker to Puebloan culture. Seltzer's work is statistical, his tables are presented, and his conclusions are thus subject to immediate check. It is obvious that Seltzer is correct and, as he points out, the Southwestern anthropologists have been guilty of very loose use of such terms as long heads and round heads.

This is, then, a most valuable paper, if only because it clears out a mass of assumptions and sets us on a sounder footing. It is also of theoretical interest to all students interested in rates of change of physical type over periods of time.

GEORGE CARTER

THE INDIAN BACKGROUND OF COLONIAL YUCATAN. *Publication 548.*

By Ralph L. Roys. Carnegie Institution of Washington, Washington. $2.75 (cloth); $1.75 (paper). vii + 244 pp.; 2 maps; 6 plates. 1943.

When Francisco Hernandez de Cordoba discovered Yucatan in 1517 he found evidence of a culture definitely superior to any which the Spaniards had previously met in the new world. The purpose of Roy's excellent book is to draw a picture of what was actually still alive of Maya civilization, the highest preColumbian development we know of, at the time of Spanish conquest. The author reviews all possible aspects of the problem such as social and political organization, customs, agriculture, industries, commerce, religious and scientific lore, etc. Though many of Mr. Roy's data have been available already in the works of Gann, Means, Thompson, Tozzer, and others, his systematic survey is a most welcome contribution to Maya studies. The most original parts of the book are an analysis of the integration of the native nobility into the Spanish governmental structure, and of the Mani land treaty of 1557, the earliest authentic Maya document written in European script. Beautiful illustrations, a glossary, bibliography, and index complete the valuable publication.

ERWIN H. ACKERKNECHT

ARCHAEOLOGY OF NORTHWESTERN VENEZUELA. *Papers of the Peabody Museum of American Archaeology and Ethnology, Harvard University, Volume XXVI, Number 1.*

By Alfred Kidder, II. Peabody Museum of American Archaeology and Ethnology, Cambridge. $3.75 (paper). viii + 178 pp.; 1 map; 18 plates. 1944.

This is a technical archeological paper. It is based on field work done by the author in northwestern Venezu-

ela at various widely distributed sites. The principal work was done in the vicinity of Lake Valencia in the northern part of the country. Here extensive excavations were made.

In addition to excavations, the literature of the early historic contacts with the Indians is surveyed, the published work of the other workers in the field is included, and many of the collections of fellow archeologists were studied. The principal part of the publication is, however, a careful and detailed presentation and discussion of the artifacts recovered and the burial practices met with at the different sites. There are ample, excellent illustrations. No data is given on the abundant skeletal material excavated.

It is clear that Venezuelan archeology, although it presents a most attractive field for study because of its geographic location in a crossroads position, has been badly neglected. This work serves to indicate the presence of several treams of influence. The presence of Amazonian, Central American, and Middle American influences are noted. The author uses excellent judgment in refusing to push his correlations. He does outline possibilities and probabilities, and indicates what is needed in the way of future work. This publication will be basic to future archeologic work in Venezuela.

GEORGE CARTER

THE PEOPLE OF ALOR. *A Social-Psychological Study of an East Indian Island.*

By Cora Du Bois. With Analyses by Abram Kardiner and Emil Oberholzer. University of Minnesota Press, Minneapolis. $7.50. xvi + 654 pp.; 32 plates. 1944.

Alor is a small island of the Netherlands Indies about half-way between Java and New Guinea. Its people are Melanesians who have been influenced by the higher cultures and races of the Greater Sunda Islands.

The book comprises four parts. In the first part, which is short, the author and Abram Kardiner state the problems. This is followed by a description of the social structure of Alor. Part Two, entitled "Psycho-Cultural Synthesis," presents the cultural material which is organized about the life cycle of the individual. Here we follow the Alorese from birth to death and learn about their relation to the various institutions of their society at each stage.

Part Three, which makes up more than half of the volume, contains eight autobiographies collected by the author. These are important contributions to our knowledge of how primitive peoples think and feel. Each biography is followed by a psychoanalytic analysis from the pen of Abram Kardiner.

Part Four, "Descriptive Norms and Ranges," presents the results of Porteus Maze Tests, word associations, and children's drawings, and an interpretation of the Rorschach experiment by Emil Oberholzer. The book is the product of full collaboration between an anthropologist on the one hand and psychologists on the other.

The People of Alor belongs to those studies which deal with the interrelations of culture and personality. Different societies have different basic, or *modal*, personalities (the term *basic personality* was coined by Kardiner, while the term *modal personality* was coined by Du Bois). These cannot be explained by inherited racial characteristics. They are the result of common cultural pressures upon the developing individual. The central task of the author consists therefore "of tracing through with as much consistency as possible the repeated and standardized experiences, relationships, and values which occur in many contexts and to which most individuals are exposed during various stages of their development, when their resources vary."

The book is a most valuable source of ethnographic material about institutions, as the informants freely described these, whereas they were reluctant—the men less so than the women—to discuss their inner feelings and reactions. The author used the technique of the psychoanalytic interview and met her informants for one hour in the morning. Each session began with the narration of the dream of the previous night. This procedure was facilitated by the Alorese habit of remembering and discussing dreams. The informant was encouraged to talk about his childhood and describe his feelings.

The results of the various approaches to the Alorese personality—involving close collaboration between several experts and the use of scientific methods—show a fundamental agreement.

It is certain that this book will become a classic among studies of the relationship between culture and personality.

K. J. PELZER

THE PEOPLES OF FRENCH INDOCHINA. *Smithsonian Institution War Background Studies Number Nineteen.*

By Olov R. T. Janse. Smithsonian Institution, Washington. 25 cents (paper). iv + 28 pp. 1944.

Recent events have brought French Indochina into the limelight, so that this well illustrated booklet in the series of War Background Studies published by the Smithsonian Institution proves extremely timely.

French Indochina comprises four protectorates—Tonkin, Annam, Laos, and Cambodia; one colony, Cochin-China; and the leased territory of Kwangchowan on the Luichow Peninsula of the Kwangtung Province. After a brief resumé on topography, climate, hygiene, natural resources, transportation, harbors, and history, the author deals with the various racial groups of Indochina. Since time immemorial Further India

has been a crossroads of peoples and cultures. The peoples of Indochina may be divided into two main groups: 1) the peoples of the plains and the Mekong valley, and 2) the peoples of the mountains. Numerically the most important people are the Annamites, who are culturally and physically closely related to the Chinese; they number about 17,000,000 souls or nearly three-fourths of the total population. They live in the plains of Tonkin, Annam, and Cochin-China. Next in importance, both politically and culturally, are the Cambodians, who number about 3,000,000. Their home is the lower Mekong Valley, especially that part included in Cambodia. They are believed to be the descendants of the Khmers, the builders of the famous monuments of Angkor. The Cambodians at one time controlled a much larger territory, but their neighbors, the Thai and Annamites, forced them to give up some of the richest sections of their kingdom.

Scattered among Cambodians and Annamites live the remnants of the once mighty Cham (some 100,000 souls), the past rulers over large parts of Annam and Cochin-China. Other important peoples of the plains are the Laotians, the Chinese—most of whom are immigrants or descendants of recent immigrants—the Malays, and Indians.

The two-and-a-half million mountain people comprise a whole series of tribes that can be divided into two groups, a northern and a southern group. The northern group is formed by tribes who immigrated in historic times from southwestern China, while the southern group comprises the real aborigines of Indochina, the Indonesians—also referred to as proto-Malays or Moï. While the plains people are permanent-field cultivators who grow lowland rice especially, the majority of the mountain folk are shifting cultivators who plant chiefly upland rice, corn, sweet potatoes, and beans in a forest clearing, or *ray*.

Since the publication of this study, France has announced that after the present war French Indochina will become the first dominion in the French Commonwealth of Nations. Will France be able to carry out its promise of "no racial, religious or national discrimination" in the face of a very aggressive Annamite majority which considers itself far superior to all other indigenous racial groups?

K. J. PELZER

EARLY MAN AND PLEISTOCENE STRATIGRAPHY IN SOUTHERN AND EASTERN ASIA. *Papers of the Peabody Museum of American Archaeology and Ethnology, Harvard University, Volume XIX, Number 3.*

By Hallam L. Movius, Jr. Peabody Museum of American Archaeology and Ethnology, Cambridge. $3.75 (paper). ix + 125 pp.; 1 map; 1 table; 18 plates. 1944.

This is a synthesis of the recent work in the paleolithic archeology of southeast Asia. It is of great value in that it brings together a mass of scattered papers and presents the results in an orderly and digested form. The grasp of the material is greatly aided by large figures that show the correlation of geology, climate, fauna, and archeology.

The discussion is regional. Northwest India, Upper Burma, Northern China, and Java are considered in turn, their probable correlations are discussed, and then the general problem is summed up. For each area the geologic happenings of the Pleistocene are discussed, and the paleolithic implements are placed within this framework. It is the author's contention that one can not order cultures primarily by their artifacts, since these are essentially social phenomena. One must depend on such natural science aids as geology, climatology, glaciology, and paleontology. By using these aids, Movius makes a generally convincing effort to show the relations between the various cultures of the areas discussed.

From this work one gets a view of the differences in the culture developments of southern and eastern Asia as opposed to the developments of Europe and Africa. Asia is characterized by a chopping-tool complex quite different from the European. It is pointed out that this is correlated with different types of men, the Sinanthropus-Pithecanthropus men as opposed to the European paleolithic men.

The divisions of the Pleistocene used are: lower Pleistocene, first glacial and interglacial; middle Pleistocene, second glacial and second interglacial; upper Pleistocene, third glacial, third interglacial, and fourth glacial. This seems an unusual division, for it shortens the lower Pleistocene and lengthens the upper. If one follows the theory recently elaborated by Simpson of the origin and divisions of the glacial period, it is much more reasonable to place the first two glacials in the lower Pleistocene, the second interglacial then becomes the middle Pleistocene, and the last two glacials make up the upper Pleistocene. Movius' evidence makes it very clear that the second interglacial is of great length in Southeast Asia. His temperature and pluvial data also fit the Simpson theory. Although this is largely a matter of terminology, it also affects somewhat the relative antiquity of the cultures involved.

GEORGE CARTER

BIOMETRY

VITAL STATISTICS OF THE UNITED STATES 1942. *Part II. Natality and Mortality Data for the United States Tabulated by Place of Residence.*

Prepared under the supervision of Halbert L. Dunn. U. S. Department of Commerce, Bureau of the Census; United States Government Printing Office, Washington. $2.00. iii + 533 pp. 1944.

In 1937 the Vital Statistics Division undertook the difficult but important step of tabulating the birth certificates by residence of the mother and the death certificates by residence of decedent. These tabulations did not replace those hitherto made on a place-of-occurrence basis, but rather supplemented them. The annual statistics have, since that date, been published in two volumes, Part I being on a place-of-occurrence classification and Part II on place-of-residence. The present volume is Part II for 1942.

The value of this new series on a residence basis is very considerable. The development of strong urban hospital centers and the general lack of hospital facilities in rural areas have been important factors in drawing people to the cities for medical care. When the births actually occurring in the cities are divided by the urban population, as was done prior to 1937, a birth rate is obtained that exaggerates the rate of reproduction in the area. There is, of course, a corresponding deficiency in the rural rate when computed on this basis. For many, although not all, purposes rates on a residence basis are a more satisfactory index of the vital facts for a population than those on occurrence. For certain studies, such as use of hospital facilities, the differences between the occurrence and residence figures are of importance.

Some indication of the amount of re-allocation is given by the following figures: Of approximately 1,400,000 deaths in 1942, about 250,000 or 18 per cent occurred in a place other than the usual residence, and of the 2,800,000 births, more than 700,000 or 26 per cent occurred away from the usual place of residence of the mother. Of the births to rural residents, 30 per cent occurred in urban areas, making the births occurring in urban areas 22 per cent higher than those to residents alone. There is a large variation between states as to the importance of residence allocation; in some cases, the difference between occurrence and residence figures is much larger than those quoted for the country as a whole, while in others the difference is trivial.

The vital statistics are presented in thirty-one basic tables, in which live births, stillbirths, total deaths, and infant deaths are subclassified in considerable detail on geographical and biological axes. These cannot be enumerated completely here, but their scope may be indicated by a partial list of classifications for live births. These include sex of child; age, race and nativity of mother; order of birth, month of birth, cases of plural birth with number born alive and stillborn; state of residence by urban and rural areas, and attendance at birth. Many of these items are cross-tabulated. Almost equally extensive tabulations are given for the deaths.

Students of the dynamics of population will be gratified that the war has not necessitated the breaking of this excellent series of annual publications.

MARGARET MERRELL

DE OMNIBUS REBUS ET QUIBUSDEM ALIIS

ARCTIC MANUAL.

By Vilhjalmur Stefansson. The Macmillan Company, New York. $3.00 xvi + 556 pp. 1944.

Prepared for the Army Air Corps by the great Arctic explorer, Vilhjalmur Stefansson, and his staff, no one will question the authoritative character of this book. When it is added that it surveys all aspects of life in the North and that it is readable and well organized, no higher praise is needed. Its one notable omission is illustration. Except for the thirteen plates of photographs showing how to build a snowhouse and to make a snow camp, the book is without pictures. Yet something had to be sacrificed to provide so full a manual of information at so reasonable a cost.

The chapters deal with the region's historical background; physical geography; climate and weather; natural light; animal life; vegetation; shelter, heat, and artificial light; food and drink; clothing and personal equipment; health, accident, and disease; travel; transportation; hunting and fishing; and mechanized transport. Biologists will be specially interested in the notes on wild and domestic animals, fishes, and insect pests and parasites. Stefansson's observations include many that are new and valuable. The discussion of vegetation is less extensive but also illuminating. The chapter on climate and weather is of ecological significance; that on health, accident, and disease has information on diet, exercise, first aid, diseases, and monoxide poisoning.

The extraordinary interest of this book is apparent at almost any page to which one may open. Whether it is a brief discourse on eating fat, the importance of keeping clean shaven, colds, or the selection of dogs, the remarks are pungent and clear as Arctic air, flavored with good humor and keen understanding.

BENTLEY GLASS

THOMAS JEFFERSON AND THE SCIENTIFIC TRENDS OF HIS TIME. *Chronica Botanica, Volume 8, Number 3. By Charles A. Browne. The Chronica Botanica Co., Waltham; G. E. Stechert and Company, New York.* $1.25 (paper). 361–424 pp. 1944.

It is the introduction of Browne's little monograph, rather than the bulk of his study, which corresponds exactly to the title of his booklet. In the introduction Jefferson is shown as one of the numerous statesmen-scientists of his time. The utilitarian and conservative character of Jefferson's scientific orientation are emphasized. Then Jefferson's *Notes on the State of Virginia* are analyzed for their scientific content and merits. Jefferson's role as promoter of science while President of the United States is recorded. Special attention is given to Jefferson's achievements as a

scientific agriculturist. The study ends with a description of Jefferson's work in furthering scientific education. Nothing essentially new is added to the extensive literature on Jefferson, the scientist; but the excellent standards of scholarship displayed, the adequate presentation of a fascinating subject matter, the easy accessibility of material, otherwise rather hidden or widely dispersed, will undoubtedly make many friends for this little book.

ERWIN H. ACKERKNECHT

A SURVEY OF GENERAL AND APPLIED RHEOLOGY.
By G. W. Scott Blair. Pitman Publishing Corporation, New York. $4.00. xvi + 196 pp. 1944.

Rheology is defined by the author as the study of the "flow and deformation of matter," or more narrowly, of the "stress-strain-time relations" in materials with "behaviour intermediate between those of solids and liquids." To biologists interested in the physical characteristics of protoplasm or protoplasmic products, this introduction to the science should be highly valuable.

The volume opens with a historical introduction, of general interest. Biologists, in particular, will find instructive the discussions of irreversible breakdown, structural viscosity, thixotropy, false body and related and converse phenomena; of mesomorphic states, tactoids, and coacervates. Aerodynamics, the rheological properties of polymers, and other topics discussed adequately elsewhere are not included. In part II, first, rheological interpretations are examined from the points of view of theory and practice; and second, considerable space is devoted to the place of "psychophysics" in rheology. Without question, subjective judgments based on differences in perception must play a significant role in this science. Scott Blair's experimental approach to the study of these is most interesting. In another chapter, the author undertakes to apply Gestalt psychology to rheology, reaching the conclusion that qualities such as "tackiness" have the nature of a Gestalt, and, in general, that each unit is to be appreciated in its spatial and temporal context.

This book could be critically appraised only by a team comprising at least a physicist, a biophysicist, and a psychologist. It is, however, apparent that it will be interesting to many biologists. The integration of special sciences undertaken by the author should prove most stimulating.

BENTLEY GLASS

MEET THE ELECTRON.
By David Grimes. Pitman Publishing Company, New York and Chicago. $2.00. vii + 120 pp. 1944.

For laymen, the author has surveyed the science of electronics in simple language and with graphic illustrations. This is just the book for a high school student or college freshman who is becoming interested in electronics, or for anyone with little or no acquaintance with physics who desires an introduction to a field of rapidly enlarging utility. It will not be of much value to biologists.

PHOTOMICROGRAPHY IN THEORY AND PRACTICE.
By Charles Patten Shillaber. John Wiley and Sons, Inc., New York; Chapman and Hall, Ltd., London. $10.00. viii + 773 pp. 1944.

The art of photomicrography involves three important steps, namely, correct manipulation of the microscope, a thorough understanding of lighting techniques, and the mounting and handling of specimens on the microscope stage. As the author points out, in most cases failure to produce good negatives is the result of poorly aligned equipment. One of the aims therefore of the present volume is to instruct the reader in the proper and precise alignment of all optical parts. Since this necessitates a thorough knowledge of the construction and function of the various elements of the optical system, the greater portion of the book is concerned with this important topic. Throughout the text there has been no separation of photomicrography and microscopy, since the same fundamental knowledge applies equally to both. In photomicrography, the sensitive film replaces the eye.

Space has been wisely given to a discussion of mounting media, stains, reagents, and solvents, and their purpose and application in photomicrography. "The photomicrographer should have a general bird's-eye view of the possibilities of all mounting methods as applied to various branches of medicine, minerology, metallography, and other scientific studies, to the end that he will be able to adopt or adapt, wholly, in part, or in combination, the various techniques of staining, etching, chemical reaction or crystallization for his own purpose."

The final chapter is devoted to an analysis of practical photomicrographical problems. A wide variety of specimens and the techniques involved in their handling is very well illustrated. It is here that the majority of the 140 photomicrographic illustrations appear. Several of them show the results of specimens under varying techniques, lighting arrangements, lens systems, etc. For convenience this chapter has been divided into eight parts depending upon the type of specimen and the microscopic technique involved, e.g., specimens photographed at magnifications of 50 diameters or less; histological specimens; metallographic and petrographic specimens; etc.

While the author is to be highly commended for his unusually clear treatment of a very technical and diffi-

cult subject, it is regrettable that he purposely chose to omit any mention of branches of photomicrography such as work with polarized light, color photography, ultraviolet and infra-red radiation, and stereoscopic pictures. However, in spite of this omission the volume is a most welcome contribution to microscopy and photomicrography. The wide variety of useful information together with an abundance of well chosen illustrative material in the form of photographs of apparatus, diagrams, tables, etc., all go to make this book especially desirable for beginners, teachers, and the more professional microscopist and photomicrographer.

JOHN SPURBECK

NATURE AND CAMERA. *Summing Up Fifty Years' Experience of Photographing Flora and Fauna.*

By Oliver G. Pike. The Focal Press, London and New York. 13s 6d. 262 pp. 1943.

One hundred and fifty-seven photographs, numerous pictorial diagrams and, most important of all, fifty years of experience in nature photography are condensed into this relatively small volume, providing much useful information for those interested in taking pictures out of doors.

The well-chosen photographs by the author and other prominent nature photographers illustrate the great variety and wide range of pictorial expression in this field. The author points out that the development of modern miniature cameras, roll film, exposure meters, and range finders is of great advantage in that it enables the photographer to devote more freedom and attention to the subject itself, whether bird, flower, or beast.

After a brief discussion of the equipment necessary in nature photography, the author gives concrete suggestions on the actual methods of procedure with various natural subjects such as flowers, birds, bird nests, mammals, fish, reptiles, insects, etc. From all of this we are led to see that nature photography is more a blend of the right approach and a few simple "tricks" than an elaborate specialized technique. Given the time and patience and the desire to study habitats of natural subjects, almost anyone who knows how to use a camera at all can develop an interesting hobby and obtain unusual and original photographs.

HACKH'S CHEMICAL DICTIONARY (*American and British Usage*) *Containing the Words Generally Used in Chemistry, and Many of the Terms Used in the Related Sciences of Physics, Astrophysics, Mineralogy, Pharmacy, Agriculture, Biology, Medicine, Engineering, etc. Third Edition.*

Edited by Julius Grant. The Blakiston Company, Philadelphia. $12.00. xii + 925 pp. 1944.

This complete revision of an indispensable standard work has been carried out, following the death of Ingo Hackh, by his British collaborator in the earlier editions. By omitting pronunciations, as to which every scientist is a law unto himself anyway, space has been saved for many additions without increasing the bulk of the volume. It now includes over 57,000 definitions. Special effort has been made to balance British and American points of view. Probably no reference book will be more generally useful to the biologist than this. It contains not only definitions of chemical and physical terms, with numerous tables, illustrations, and diagrams, but also much biographical and biological material. Its standard of accuracy is high. Its type is well chosen for legibility.

PACIFIC OCEAN HANDBOOK. *Second Edition.*

By Eliot G. Mears. James Ladd Delkin, Stanford University. $2.00 (cloth); $1.00 (paper). x + 198 pp.; 1 map. 1944.

This little handbook presents a wealth of facts pertaining to the Pacific area. It is profusely illustrated with maps, charts, diagrams, and a large insert containing global views of the Pacific from the west, east, and center. There are sixteen chapters describing various oceanographic, climatic, and geographic features of the Ocean and its coastlines. Such topics as volcanoes, earthquakes, tides, currents, winds, storms, temperature, precipitation, fog, and geomagnetism are briefly discussed. In addition, there are short references to the major ports on both sides, some pointers on navigation, and on the characteristics of sea water. Twelve appendices give further factual data on areas and population, airline distances, food plants and animals, hints for the shipwrecked, etc. It is obvious that to cover so much material intensive condensation was required, and in some sections the presentation suffers accordingly. However, it should provide helpful information to those now active in the Pacific area. "The second edition has been enlarged to include additional information, appendices on coral islands and on monsoons, as well as a more complete index. The majority of maps have been redrawn to make them clearer . . ." The author will welcome information based on first-hand observations and experiences within the Pacific area.

ANNUAL REPORT OF THE BOARD OF REGENTS OF THE SMITHSONIAN INSTITUTION *Showing the Operations, Expenditures, and Condition of the Institution for the Year Ended June 30, 1943. Publication 3741.*

United States Government Printing Office, Washington. $2.00. xi + 609 pp. 1944.

In addition to the annual report, this volume contains an appendix of twenty-three papers of considerable general interest. Three of these, "The Natural History Background of Camouflage" by Herbert Friedmann, "Dangerous Reptiles" by Doris M. Cochran, and "Origin of the Far Eastern Civilizations" by C. W. Bishop are reprinted from the excellent series of Smithsonian War Background Studies. Other papers of biological interest deal with the biological effects of solar radiation, plants of China and their usefulness, natural rubber, lessons from Old World land use, areal and temporal aspects of South American culture, culture contours in Indonesia, the Arab village community of the Near East, chemotherapeutic agents from microbes, sulfonamides in the treatment of war wounds and burns, the yellow fever situation in the Americas, and food problems of wartime. Other articles deal with solar radiation for power, oceanography, petroleum geology, maps, synthetic textile fibers, new metals, and the sea as a storehouse of materials.

The style of the papers is in general non-technical, resembling that of articles in the *Scientific Monthly*. Numerous plates and maps help to make the discussions informative. Altogether, it is a volume that will be stimulating and useful to the biologist.

MAUD DE WITT PEARL

MAY 3, 1879—AUGUST 10, 1945
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1936–1945